THE ENVIRONMENTAL VARIABLES OF THE MISSOURI BOTANICAL GARDEN WILDFLOWER RESERVATION AT GRAY SUMMIT[1]

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INTRODUCTION

Included in the 1,296-acre tract representing the Arboretum of the Missouri Botanical Garden is a parcel of land, roughly 300 acres in extent, which has been set aside to be developed as a wildflower reservation. Here the native trees, shrubs and herbs peculiar to the various natural habitats will be brought together where the public can readily become acquainted with them. Here also rare or otherwise uncommon indigenous wild plants will be held safe from extinction by the hands of the predatory tourist.

It is the purpose of this paper to present a preliminary survey of some of the more important factors conditioning the various environments represented in the Wildflower Reservation of the Missouri Botanical Garden in order that its development may be carried on in a systematic manner. It is hoped that this investigation, despite its strictly elementary nature, will indicate the more important factors to be studied specifically and critically at some future date. An attempt will be made also to correlate the extant arboreal vegetation with the various environmental factors in order to arrive at bases for interpreting the distribution of the native flora. In the course of this study the geology, physiography, soils, and climatology of the area were investigated and the alteration of the flora by the activities of man was reviewed.

For the purpose of this study an area was selected which embraced the various habitats characteristic of the reservation as a whole. The area chosen is bounded on the north by a service road commonly known as the Ridge Trail, on the south by a line connecting the face of the cliff terminating Cliff Ridge to the east with the ledge terminating Ledge Ridge to the west. A line drawn down the

[1] An investigation carried out in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, under the direction of Prof. Lewis F. Thomas and Dr. Edgar Anderson, and submitted as a thesis in partial fulfillment of the requirements for the degree of master of science in the Henry Shaw School of Botany of Washington University.

crest of Cliff Ridge forms the eastern boundary of the area. A similar line drawn down the crest of Ledge Ridge bounds the area to the west.

GEOLOGY

The area lies on the northern border of the region of dolomitic limestone rocks which compose the greater part of the northern Ozark plateau. The rocks belong to the Canadian Series of the Lower Ordovician Period.[2] Two formations are represented, the uppermost stratum of the Jefferson City formation, and the Cotter formation.

METHOD OF STUDY

The rugged land-form of the area and the numerous outcrops of the bed rock made the study and accurate mapping of these outcrops comparatively easy. The cliff terminating Cliff Ridge on the east side of the area offered an excellent exposure for studying the stratigraphy. The thickness of the formations and their different phases were accurately measured with tape and plumb line. The rocks outcropping in the ledge that terminates Ledge Ridge on the west and the numerous outcrops of bed rock on either side of the valley dividing the area provided a sufficient number of stations for correlating the areal geology on a topographic map. A transect line was established up the valley, and from this line shorter lateral lines, at right angles, were made to the various points where outcrops occurred. The relative elevations of the different outcrops were obtained by means of a Brunton compass which was also used to measure the angles of the various slopes. Distances were paced off.

Since the two formations represented on the area are essentially dolomitic in nature, the examination of the chemical properties of the rocks was limited to a determination of the percentage of the dolomite crystals in the various formations or in such phases of these as had an apparent bearing on the vegetation.[3]

Early in this investigation it seemed advisable to study the physical properties of the various rocks, particularly those of the glades.

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[2] Weller, Stuart, and Stuart St. Clair. Geology of Ste. Genevieve County, Missouri. Mo. Bur. Geol. and Mines, II, **22**: 30–31. 1928.

[3] By polishing a smooth surface on the rock, then staining it with Lemberg's solution or molar copper-nitrate solution $Cu(NO_3)_2$, the dolomite crystals were easily differentiated from the calcite and other calcareous minerals.

Perhaps in such features as porosity and permeability might lie the basic cause for the development of the unique glade flora. The relative porosities of the various rocks were determined by gravimetric methods, using a procedure outlined by Melcher.[4] The permeabilities of the rocks were tested by comparing the depths to which a dye would penetrate in a given period of time. This procedure, though simple and providing little quantitative data, did, however, show the relative extent to which the rocks were permeable to the infiltration of ground waters.

STRATIGRAPHY[5]

The Jefferson City Formation.—The Jefferson City formation forms the lowest rock outcrop of the strata exposed in the area (fig. 1). The uppermost seven feet of this formation are exposed at only two stations, one in the mouth of the valley, the second at the base of the east end of the ledge terminating Ledge Ridge. The fact that this is the lowest of the rocks outcropping on the area has caused it to be covered with talus debris over the greater part of its range. The rock is a dolomitic limestone, for the most part massive, oolitic, and light buff to gray-brown in color. It has a comparatively low porosity, approximately 5 per cent, is quite permeable, and contains 30 per cent of dolomite crystals. No unconformities are evidenced between the Jefferson City formation and the overlying Cotter formation.

The Cotter Formation.—The remaining rocks outcropping on the area belong to the Cotter formation. Unlike the underlying Jefferson City formation, deeply overlain with talus debris, it presents a great areal exposure of bare rock surface. It was suspected that these various outcroppings, because of their different physical and chemical natures, were apt to be of direct influence on the flora. The formation is composed of phases of sandstones and dolomitic limestones. The limestones appear in both massive and thin-bedded phases, the latter being essentially ''cotton rock.''

The basal phase of the Cotter formation is one of gray to gray-red sandstone 37 feet in thickness. This sandstone, like the final

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[4] Melcher, A. F. Determination of pore space of oil and gas sands. Trans. Amer. Inst. Met. Eng. **65**: 496–497. 1921.

[5] The geological correlations made in this paper are based on a well log which is on file at the offices of the Missouri Geological Survey.

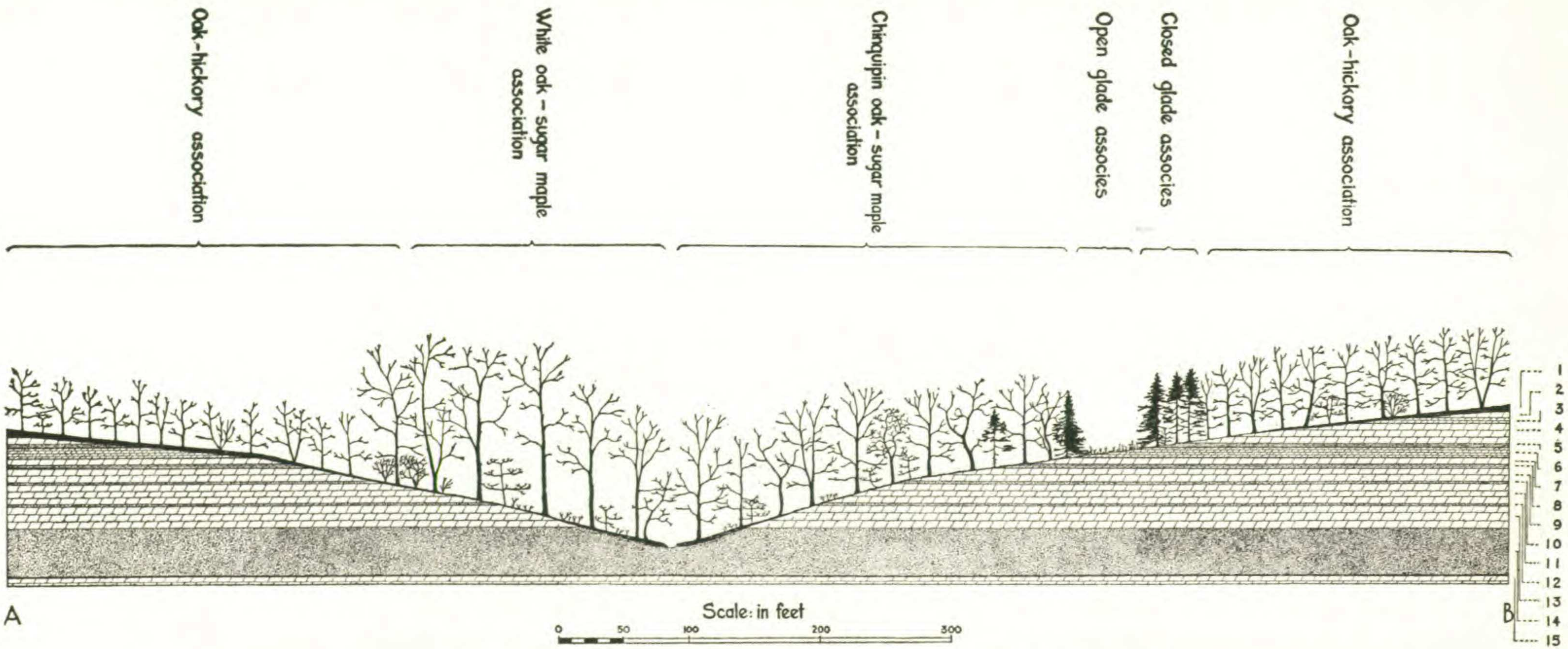


Fig. 1. Structure section through the area A–B (see fig. 2).

1. Soil—silt loam..Union silt loam
2–14..Cotter formation
2. Limestone—massive, dolomitic; 3. "Cotton rock"; 4. Limestone—massive, dolomitic; 5. Sandstone—red; 6. "Cotton rock"; 7. Limestone—massive, dolomitic; 8. "Cotton rock"; 9. Limestone—massive, dolomitic; 10. Sandstone—gray; 11. Limestone—massive, dolomitic; 12. Sandstone—gray; 13. Limestone—massive, dolomitic; 14. Sandstone—gray
15. Limestone—massive, dolomitic..................................Jefferson City formation

phase of limestone of the Jefferson City formation which it overlies, is almost entirely covered with a mantle of talus, though numerous small outcrops occur on the valley slopes and in the bed of the wash draining the valley. Overlying this sandstone phase is one of massive limestone 34 feet in thickness and having an intercalation of sandstone about 2 feet thick near its center. Like the higher massive dolomitic phases of the formation, it has a relatively small proportion of pore spaces, 5 per cent, is quite highly permeable, and contains 40 to 50 per cent of dolomite crystals. Chert nodules and lenses, white, brown, to pinkish-blue in color, commonly occur. This phase outcrops in entirety on the face of the cliff at Cliff Ridge, forming a series of high step-like ledges. On the valley walls it has been smoothed off by erosive agents and is overlain by a mantle of chert and float material from strata above. A fine-grained, gray sandstone overlies this massive phase to a depth of two feet and this in turn is overlain by a phase of massive dolomite 9½ feet thick and having a six inch phase of sandstone intercalated four feet above its base. Three feet of thin-bedded dolomite, "cotton rock," overlie this massive phase and in turn are overlain by another five feet of similarly massive dolomite and seven feet of thin-bedded dolomite. The last is typical "cotton rock," pink or buff to gray in color, easily fractured, and in beds from ½ to 4 inches thick. Exhibiting the highest degree of porosity, 24 per cent, of all the rocks occurring on the area, and composed of pure dolomite, $CaMg(CO_3)_2$, together with a very high degree of permeability, it is indeed a most interesting rock. The thin beds are intercalated with very thin lenses of sandstone and a blue-white or pink chert. Rarely, minute intercalations of shale occur between thin beds of slightly argillaceous "cotton rock."

The small remaining portion of the formation has, for the most part, been covered by the Union silt loam which caps the ridges. Outcrops of these higher and final rocks of the formation are not abundant within the area. A few occur at the head of the valley, and some have been laid bare in the construction of the trail on the crest of Cliff Ridge. The latter are thin-bedded, coarse-grained dolomite with thin lenses and nodules of chert. A phase of putty-gray shale six inches in thickness overlies the "cotton rock" and is overlain by a medium-grained, loosely cemented, gray or red-brown sandstone one to three feet in thickness. A five-foot phase of massive faintly oolitic dolomite overlies the sandstone.

TOPOGRAPHY AND RELIEF

The area, essentially rugged, is in the mature stage of the erosional cycle, a feature typical of the hills and ridges bordering the southern face of the area to the north of the Meramec River.[6] Two ridges, Cliff Ridge and Ledge Ridge, truncated by an ancient meander of the Meramec River, rise 140 feet above the flood plain of that river (fig. 2). The cliff terminating Cliff Ridge, together

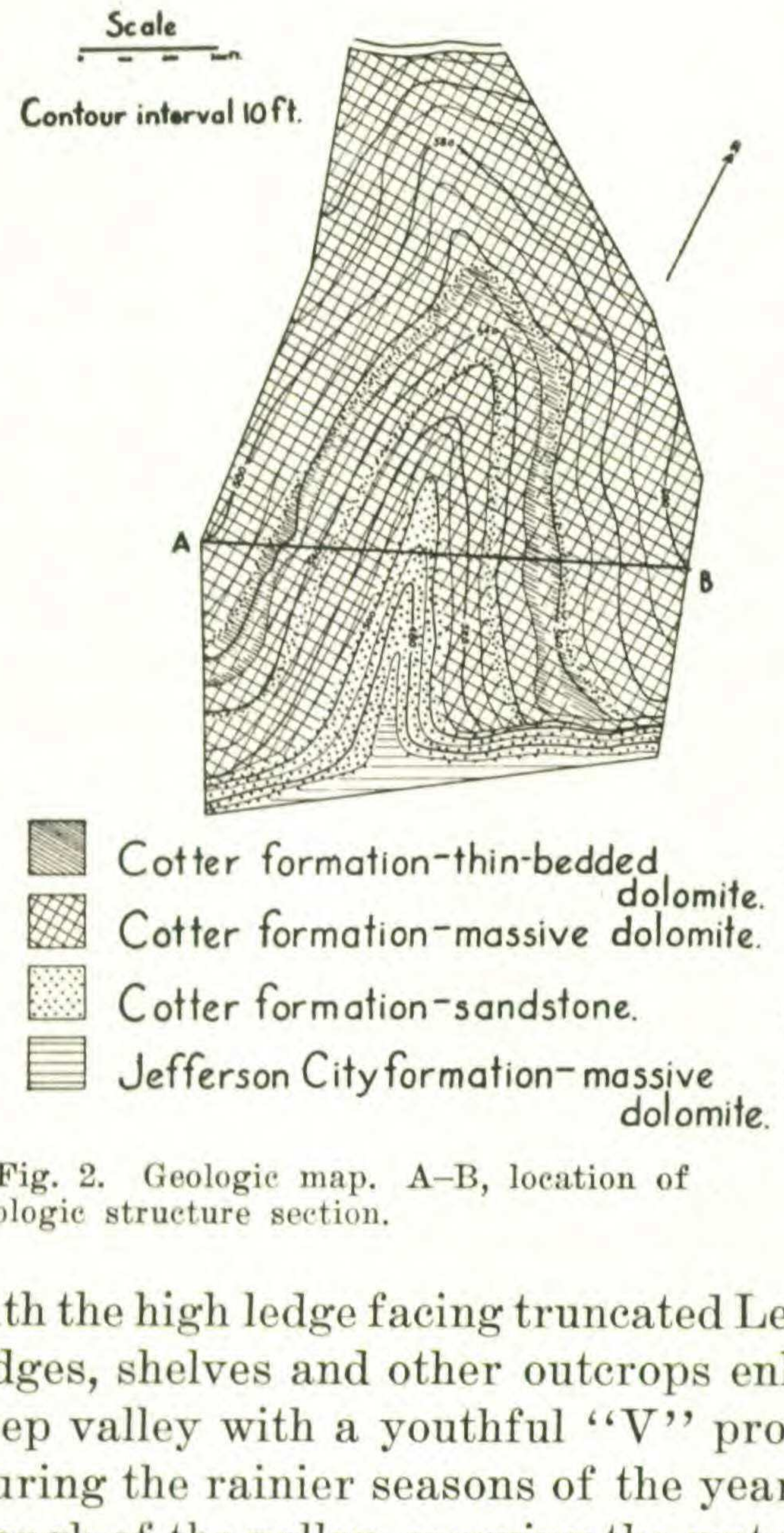


Fig. 2. Geologic map. A–B, location of geologic structure section.

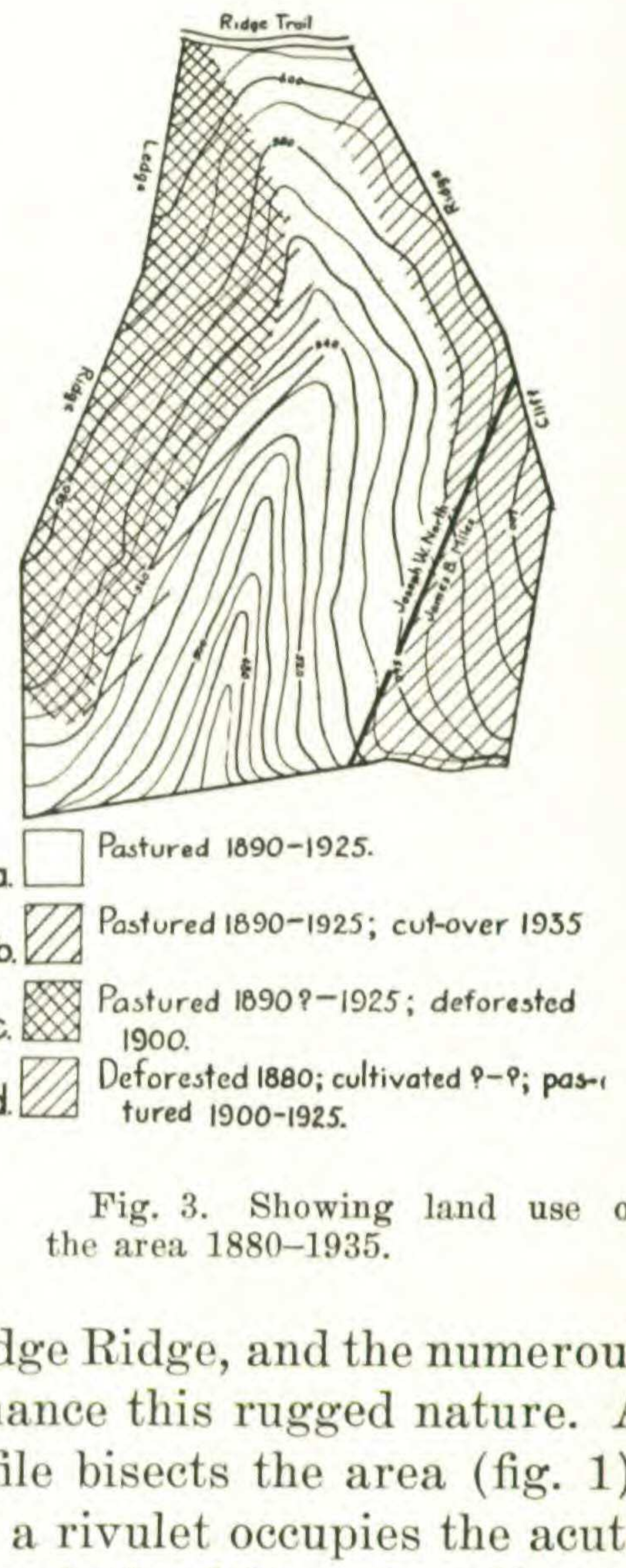


Fig. 3. Showing land use of the area 1880–1935.

with the high ledge facing truncated Ledge Ridge, and the numerous ledges, shelves and other outcrops enhance this rugged nature. A deep valley with a youthful "V" profile bisects the area (fig. 1). During the rainier seasons of the year a rivulet occupies the acute trough of the valley, carrying the waters drained from the adjacent uplands to the flood-plain where they are soon lost in the gravels underlying the silt. The ridges are, for the most part, narrow and appear as lateral spurs from the higher ridge serving locally as the

[6] Marbut, C. F. Soil reconnaissance of the Ozark region of Missouri and Arkansas. U. S. Dept. Agr., Bur. Soils and Field Operations, Rept. **13**: 1727–1873. 1911.

drainage divide between Brush Creek to the north and Meramec River.

The area, as a whole, offered an interesting study in angles of slope[7] resulting from differential weathering of the formations and their included phases. A profile of the valley, taken at points A-B (figs. 1 and 2), shows the massive limestone of the Jefferson City formation overlain by the weaker, basal sandstone phase of the Cotter formation and this in turn by the resistant massive limestone. Here the angle of slope is quite high, 15 to 18 degrees, and few outcrops occur since the rock is deeply overlain by soils creeping down from above. This steep angle of slope persists through the massive phases of the Cotter formation where it is broken by the thin-bedded phase of that formation. Here the slope is about 10 degrees. The steeper angle is resumed by the recurrence of the second massive phase of the Cotter, represented in part by a low ledge. The second, thicker of the thin-bedded phases of the Cotter formation causes a conspicuous break in the angle of slope. Here the weakly resistant, thin-bedded rocks have been rapidly beveled off, and the angle of slope is more gentle, 10 degrees. A low ledge marks the thin sandstone phase overlying the "cotton rock," after which an even lower angle of slope, 5 degrees, is assumed and retained to the crest of the ridge.

Soil Survey

The soils of the area have been classified by the United States Department of Agriculture, Bureau of Soils, as belonging to the sandy subsoil phase of the Union silt loam.[8] The report did not consider the smaller, more specialized types of soil, particularly those classified as "rough stony land." Such soils lie on the steep slopes of the ridges immediately north of the Meramec River in the vicinity of Gray Summit. Since a great portion of the area under investigation is covered by such soil, it was found necessary to study its physical and chemical properties to aid in the interpretation of the flora.

METHOD OF STUDY

Samples, weighing about 100 grams, of the upper six inches of the soil were systematically taken at 100-foot intervals across the val-

[7] Cozzens, Arthur B. Analyzing and mapping natural landscape factors of the Ozark province. Acad. Sci. St. Louis Trans. **30**: 37–63. 1939.

[8] Vanatta, E. S., and H. G. Lewis. Soil survey of Franklin County, Missouri. U. S. Dept. Agr., Bur. Soils and Field Operations, Rept. **13**: 1603–1633. 1911.

ley and at 200-foot intervals up the valley. After drying thoroughly in the air they were examined for content of organic matter, relative proportions of different sizes of soil particles, as recognized by the Bureau of Soils, and soil reaction or degree of acidity.

Analysis of Organic Content.—Ten-gram portions of the samples were taken along line A–B (fig. 2). After being weighed, they were heated in a crucible for 30 minutes over a hot Bunsen burner. They were weighed again after cooling, and any loss of weight was considered to be organic material removed by combustion. The results of these operations appear in TABLE I.

TABLE I

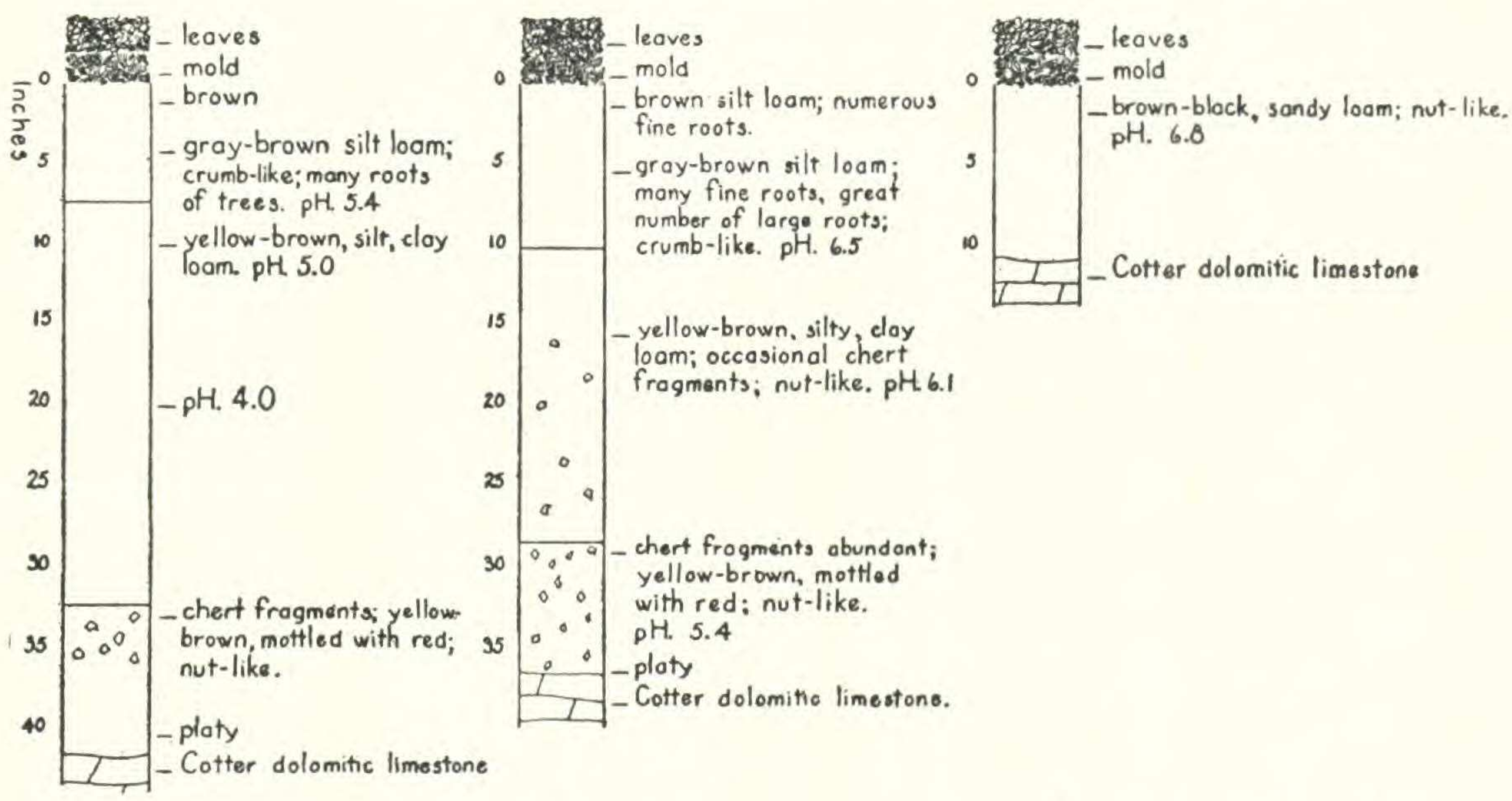
MECHANICAL AND ORGANIC-CONTENT ANALYSIS OF THE SOIL ALONG BELT TRANSECT B (see fig. 11)

Sample	% Rock & gravel	% Fine gravel	% Coarse sand	% Medium sand	% Fine sand	% Very fine sand	% Silt & clay	% Organic matter
1	0	0	.73	2.84	4.39	1.99	80.41	9.5
2	7.83	2.85	2.27	3.17	4.37	3.65	64.58	10.8
3	15.62	7.20	3.34	4.81	5.40	6.39	54.06	1.7
4 Glade	59.87	1.91	1.16	2.08	3.41	2.41	43.31	17.0
5	35.57	6.94	2.20	7.13	10.16	4.39	16.94	15.3
6	34.30	1.57	1.27	2.46	6.34	5.87	15.77	31.4
7	39.24	2.16	3.80	2.72	7.41	5.04	19.22	19.9
8	14.85	4.61	4.62	5.99	6.08	5.31	43.85	14.3
9	0	.179	1.61	4.58	4.58	5.024	73.71	10.1
10	0	.93	1.58	3.26	4.37	3.25	79.05	7.0
11	0	0	.85	3.07	4.32	3.36	84.56	3.9

Mechanical Analysis.—An analysis was made of samples taken along line A–B (fig. 2) to show the percentages of the different sizes of soil particles. Fifty-gram portions of the air-dried samples were weighed out. They were then dispersed in a mortar by gently rubbing with a pestle, after which they were shaken successively through a series of screens recommended for mechanical analysis of soils.

Soil Reaction (degree of acidity).—The samples taken over the whole area were tested for soil reaction with Brom Cresol Green, Brom Cresol Purple, and Phenol Red indicators in a method described by Moore.[9] The results are compiled in fig. 6.

Soil Horizons.—Several test pits were dug at stations covered with a typical flora and suggesting a typical soil type. Where possible the pits were dug down to bed rock, but when the soil mantle was so deep as to make this impractical the approximate depth of the soil was tested by probing into the bottom of the pit with a crowbar. The thicknesses of the various soil horizons were measured and their color, texture, consistence, structure and porosity noted



a. Union silt loam, sandy subsoil phase, Main Ridge b. Union silt loam, sandy subsoil phase, Ledge Ridge c. Rough stony land, lower slope of Ledge Ridge.

Fig. 4. Soil profiles.

in accordance with recommendations made by Kellogg.[10] Sample profiles of the typical soils are shown drawn to scale in fig. 4.

THE SOILS

As was previously stated, the soils of the area have been classified by the Bureau of Soils into two distinct groups: the sandy-subsoil phase of the Union silt loam, and the "rough stony land."

The Union Silt Loam, Sandy Subsoil Phase.—The Union silt loam, sandy subsoil phase, is a brown or grayish-brown mellow silt loam 6–8 inches deep, which changes at depths between 8 and 20 inches into a light brown or yellowish-brown friable silt loam or

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[9] Moore, W. An improved method for the determination of the soil reaction. Brit. Golf Unions Jour. 4: 136–138. 1935.

[10] Kellogg, Charles E. Soil survey manual. U. S. Dept. Agr. Misc. Publ. 274. 1937.

a silty clay loam. In structure the soil is crumb-like, grading into a nut-like subsoil (fig. 4a & b). Its origin is not perfectly understood, but its uniform nature over broad areas seems to suggest that it is loessial. An interesting character of this soil is the high proportion of fine sand grains (TABLE I). This soil lies as a cap, about 3–3½ feet deep, upon the crests of the ridges. Its loose sandy nature, together with the relatively high angles at which it lies on the slopes, has made it an easy prey to agents of erosion. In places

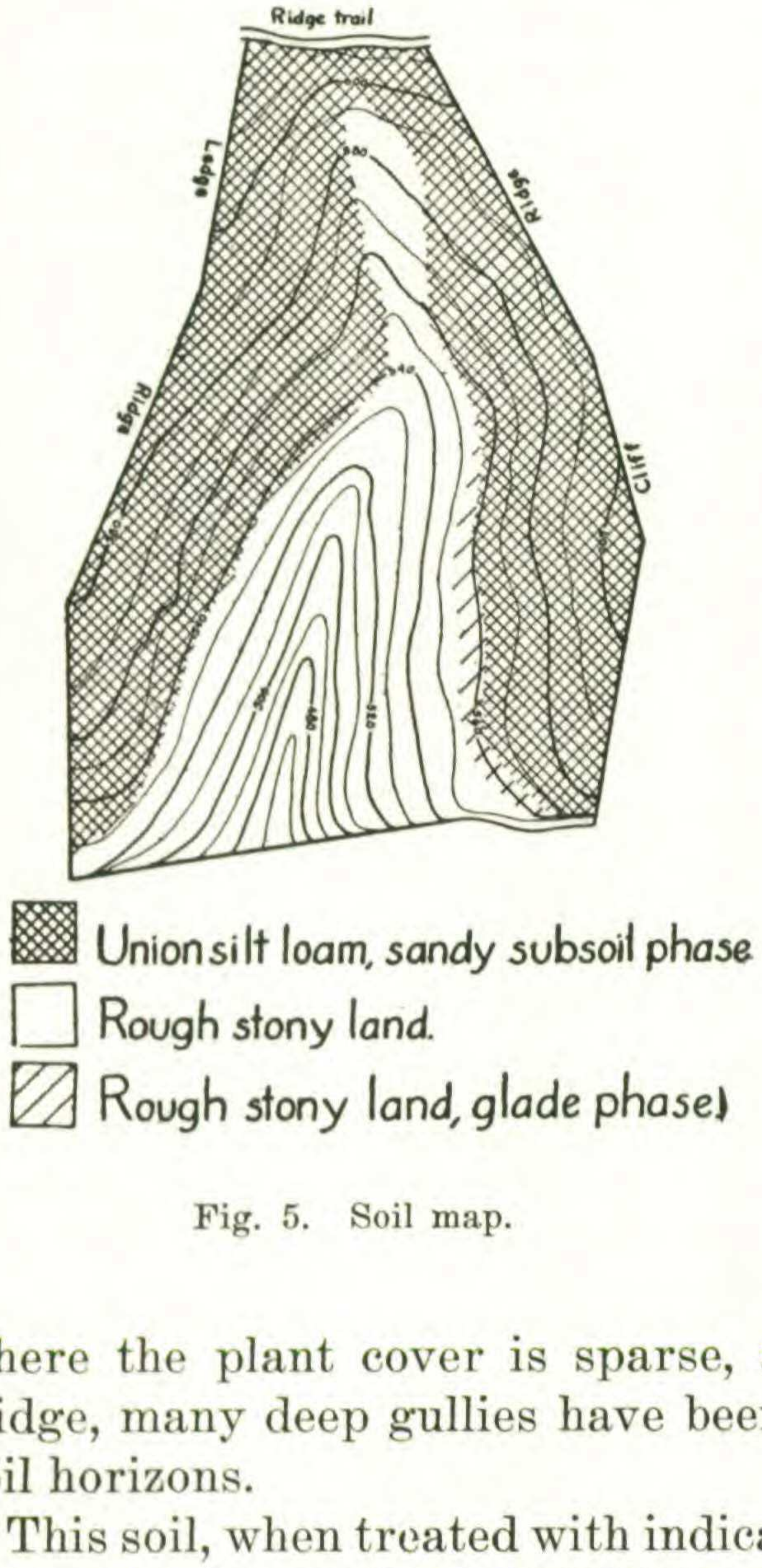

Fig. 5. Soil map.

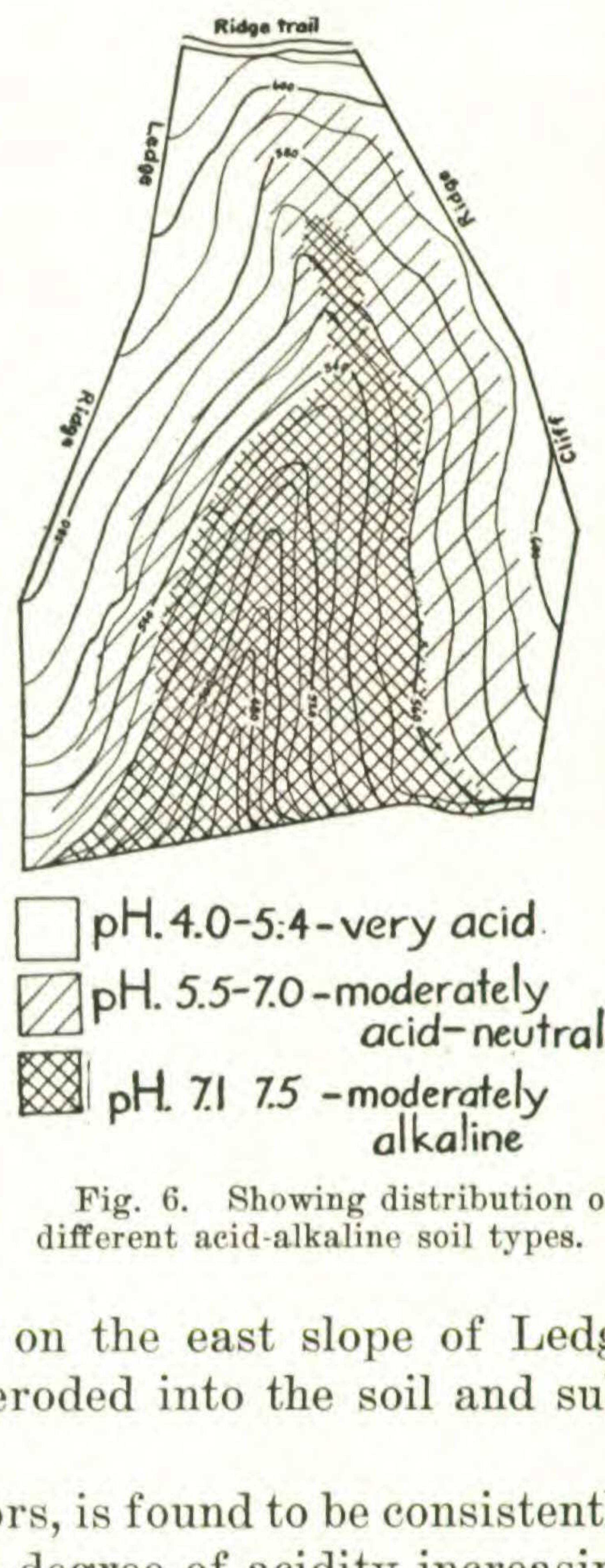

Fig. 6. Showing distribution of different acid-alkaline soil types.

where the plant cover is sparse, as on the east slope of Ledge Ridge, many deep gullies have been eroded into the soil and subsoil horizons.

This soil, when treated with indicators, is found to be consistently very acid, from pH 4.0 to pH 5.4, the degree of acidity increasing as one proceeds to the lower soil horizons (fig. 4a & b). The low pH is perhaps partly due to its sandy, porous nature which has facilitated leaching to a moderate degree. There is also a decided tendency for vegetable litter to collect on the forest floor. It is in those places where the litter has collected to a considerable depth and where it is predominantly of oaks and hickories, which is relatively slow to decay, that the lowest pH ranges are reached.

The soil shows a low content of organic matter, 1.7 to 10.8 per cent (TABLE I). The majority of the trees are of tap-root nature. Fibrous roots would tend to increase the organic content of the soil, but few such root systems are formed and they are necessarily short-lived. For the most part, few herbs are found on the forest floor on the ridges, and such plants are an important source of humus. Perhaps the poor herbaceous flora may be due to the thick layer of forest litter which prevents seeds and other propagules from reaching a suitable growth medium, particularly since the surface of this litter is dry for the greater part of the time. Also the forest floor is densely shaded during most of the growing season. Animal action in this soil is not particularly great. Comparatively few "signs," castings, burrows, or actual specimens of the more common subterranean animals were found in the course of sampling. The high degree of acidity and the low organic content of the soil might account for the poor fauna.

"Rough Stony Land."—The soil of the "rough stony land" is essentially residual and very shallow, from a mere film to 12 or 14 inches in depth. It is a very dark, brown-black to black sandy loam, plastic when wet, very brittle when dry, and essentially nut-like in structure (fig. 4c). The very shallow depth of the soil has permitted it to mature relatively early, which is indicated by the lack of definite horizons and the abundance of small insoluble fragments of chert. This soil may be considered as a vertically uniform mass. It contains a relatively high per cent of fine sand grains which increase as one progresses towards the valley (TABLE I). It is interesting to note the abundance of oolite composing these sand grains, a feature offering good evidence of the residual origin of this soil, for they have weathered out of the underlying oolitic dolomite rock strata.

This soil differs markedly from the Union silt loam of the ridges in being essentially a basic or lime soil. Soil tests show a pH range from very slightly acid, 6.8 at the uppermost limit, to alkaline, 7.5, in the valley (fig. 6). This soil contains a large amount of organic matter, 14.3 to 31.4 per cent, which increases steadily as one progresses down the slope and reaches its maximum in the valley (TABLE I). The high organic content of this soil, its shallow depth, and the massiveness of several of the underlying rock formations or their phases cause it to be exploited to a high degree by the roots of trees and herbs. The high organic content makes this soil a valuable reservoir of infiltrated water and as a consequence able to support a rich herbaceous and arborescent flora. Animals are quite active here, numerous burrows, castings, puppae and specimens being noted.

"Rough Stony Land," Glade Phase.—This soil is limited to the glade, formed by the thin-bedded phase of the Cotter formation, on the west slope of Cliff Ridge (fig. 1). It is a very thin (from a mere film to 4 inches in depth) gray-brown silt loam. Soil reaction tests show it to have a pH range from 6.8 to 7.1, an essentially neutral reaction. An interesting feature of the glade soil is its high humus content, approximately 17 per cent. This can easily be understood when one remembers that the glades are of a xeric nature and therefore unfavorable to conditions of decay. The shallow depth of the glade soil and the generally xeric conditions tend too to discourage occupancy by subterranean animals, also important agents in the reduction of organic material.

Climatology of the Area

The geomatic position of the area, between longitudes 90° and 91° West, and latitudes 38° and 39° North, places it in the temperate zone. Here the weather is governed by cyclonic conditions in winter. Local continental thunder-storms prevail in summer. The region has an annual rainfall of approximately 39 inches. The mean annual temperature is approximately 55° F. The last killing frost in the spring usually occurs about April 16, and the first killing frost in the autumn about October 22.

Accurate records of the precipitation on the area were not kept. However, a weather station at Pacific, Missouri, seven miles away, offers data which may be applied with reasonable reliability.[11]

Relatively accurate temperature records were kept on the area continuously for one year, at stations selected for extremes in environment. Thermometers were housed in specially designed shelters three feet above the ground. Comparisons were made of temperatures recorded on the ridge (Sta. A-1) and in the valley (Sta. A-2); on a west-facing slope (Sta. B-1) and an east-facing slope (Sta. B-2); on the open glade (Sta. C-1) and closed glade (Sta. C-2) (figs. 8–10). Temperatures of two-week periods were selected as representative of each season of the year. Unfortu-

[11] Climatological data, Missouri section. U. S. Dept. Agr., Weather Bureau. 1940–1941.

nately, with only two recording thermometers available, continuous records at any one station were not possible, and in order to obtain a recording representative of each season the instruments had to be moved to another station every third week. This fact has prevented the direct comparison of most of the stations at a given time.

Comparison of Temperatures on Ridge (Sta. A-1) and in Valley (Sta. A-2).—In spring the ridge tends to be cooler during the day-

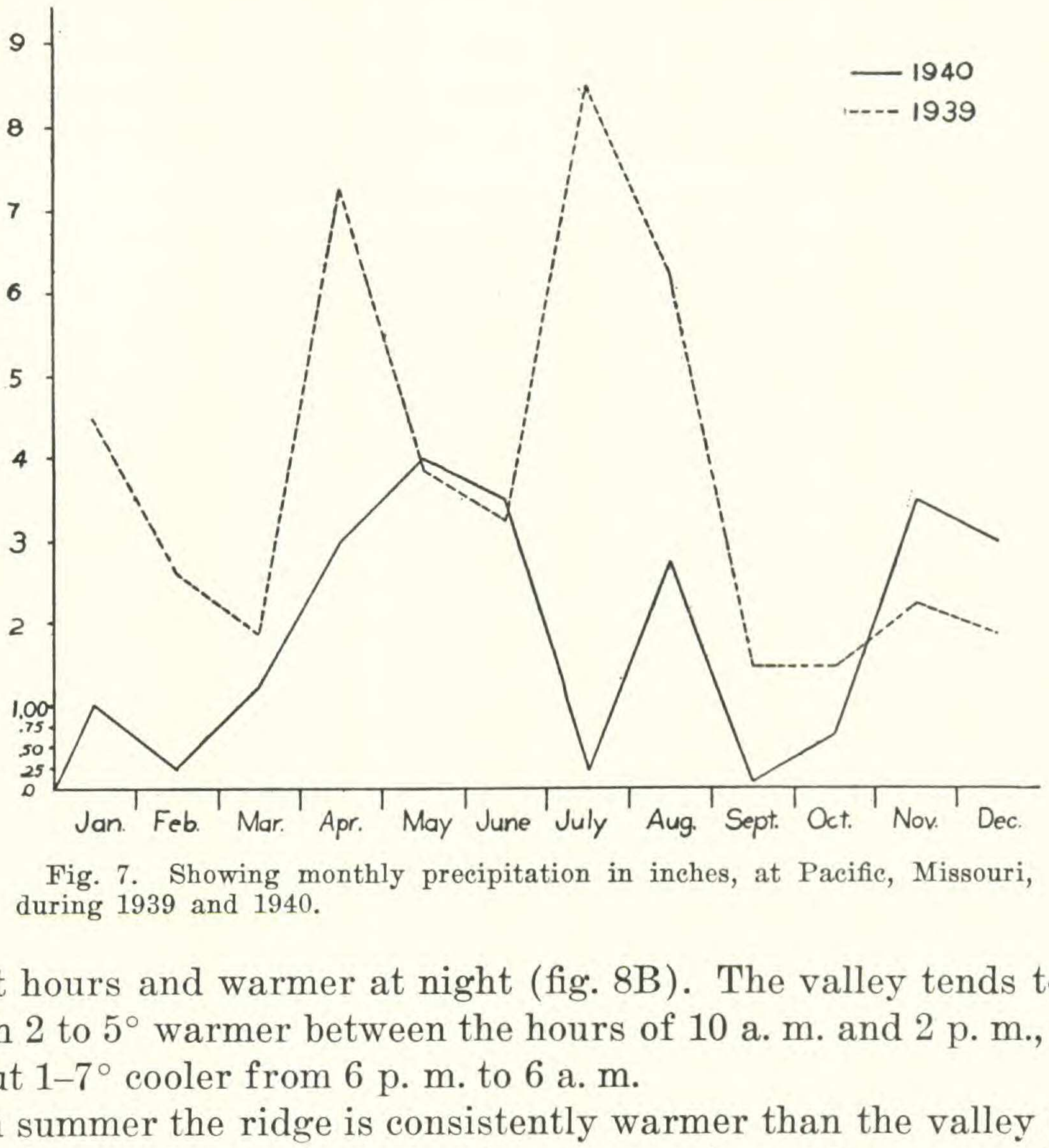

Fig. 7. Showing monthly precipitation in inches, at Pacific, Missouri, during 1939 and 1940.

light hours and warmer at night (fig. 8B). The valley tends to be from 2 to 5° warmer between the hours of 10 a. m. and 2 p. m., and about 1–7° cooler from 6 p. m. to 6 a. m.

In summer the ridge is consistently warmer than the valley (fig. 8C); in the night and very early morning, from 11 p. m. to about 6 a. m., it is usually only 2–4° warmer. For the remainder of the day, the ridge is about 5–8° warmer than the valley, except from 11 a. m. until 2 p. m., when it is only slightly warmer, 0 to 4°. The maximum mid-day temperature occurs at noon in the valley, due perhaps to the fact that after the sun drops several degrees past a vertical position the valley is again shaded by the foliage of the trees. The maximum mid-day temperature occurs at about 2 p. m.

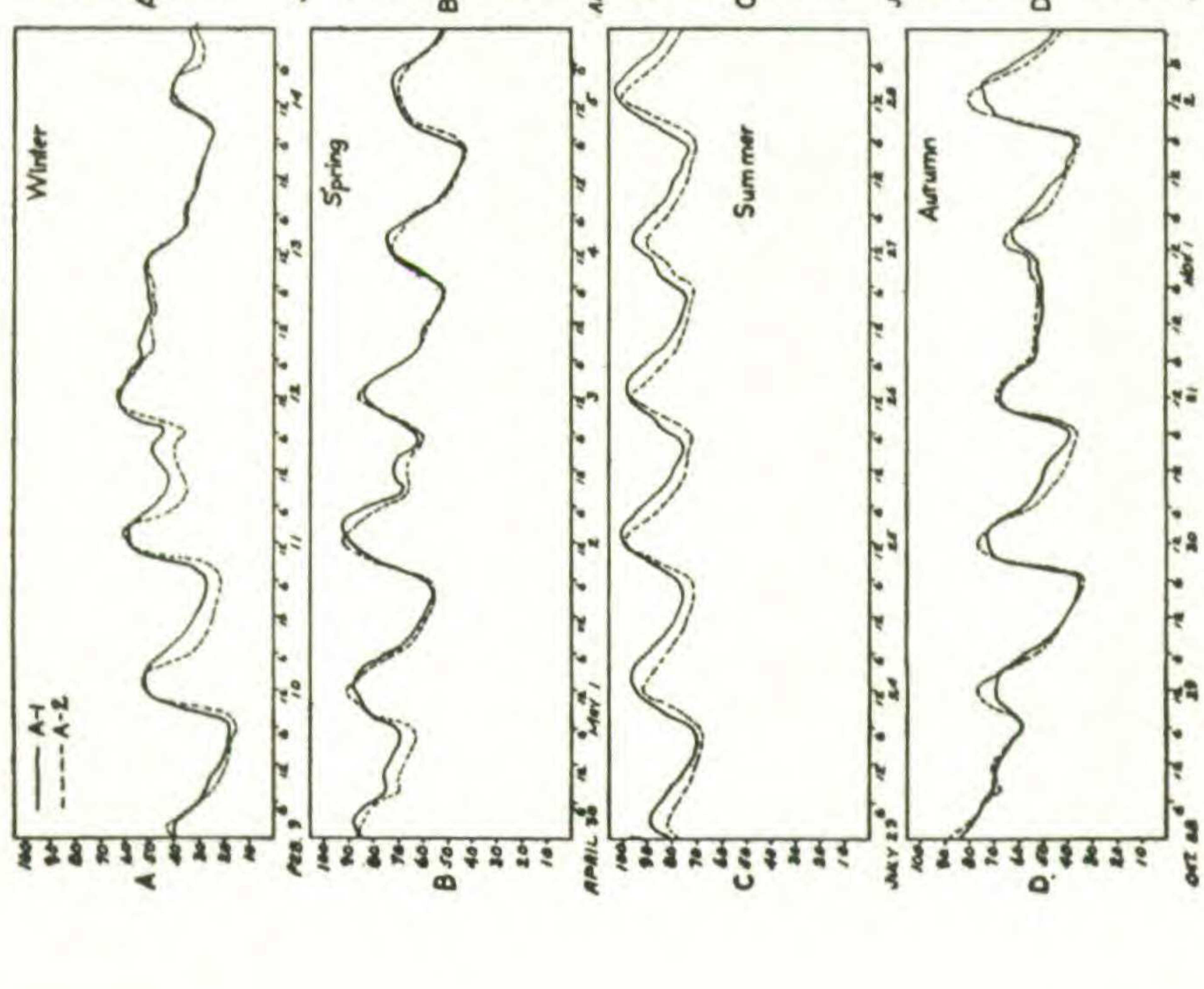

Fig. 8. Graphs of temperatures recorded as samples of seasonal variations between stations A-1 (ridge) and A-2 (valley).

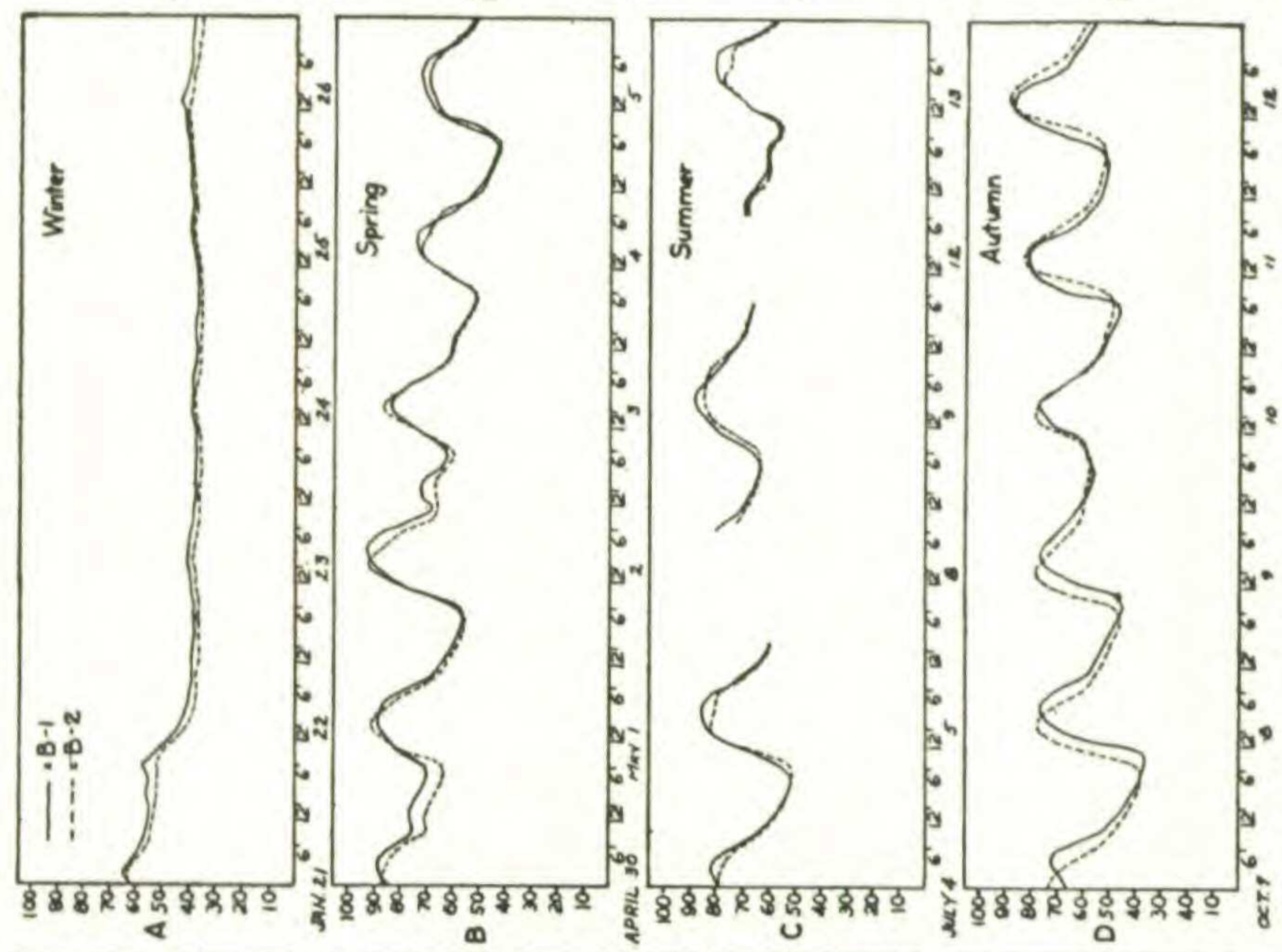

Fig. 9. Graphs of temperatures recorded as samples of seasonal variations between Stations B-1 (west-facing slope) and B-2 (east-facing slope).

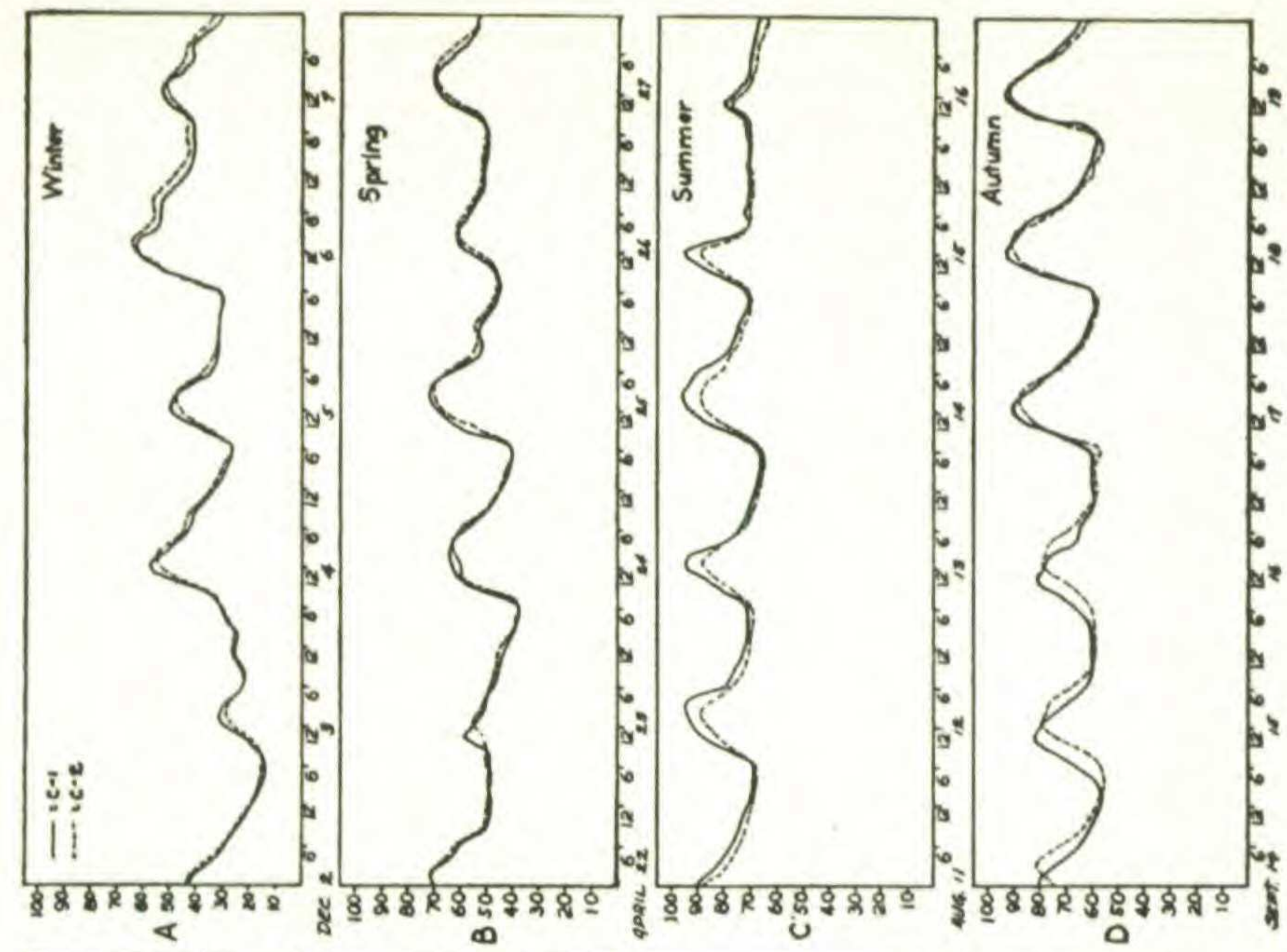

Fig. 10. Graphs of temperatures recorded as samples of variations between stations C-1 (open glade) and C-2 (closed glade).

on the ridge, where even after the sun has fallen from its vertical position it still penetrates through the less dense foliage.

With the approach of autumn and winter, the gradual loss of leaves by the trees permits a proportionately greater penetration of the sun's rays into the woods. It was noticed then that the maximum mid-day temperature in the valley was reached at noon as it was in the spring (fig. 8A and D). Similiarly, as the day temperatures in the valley increased, the night temperatures decreased. This marked difference in nocturnal temperatures is caused by the cooler, denser night air settling in the valley, a phenomenon known as air drainage. Day temperatures here tend to be 5–9° higher than those on the ridge, while night temperatures are 2–4° lower.

Comparison of Temperatures on West-facing Slope (Sta. B-1) and East-facing Slope (Sta. B-2).—In the early spring, autumn, and winter, when the trees are bare, the west-facing slope is strikingly cooler in the morning and very early afternoon, from 6 a. m. to 1 p. m. (fig. 9A, B, D). At this time the west slope was from 2 to 10° cooler than the east slope. During the late afternoon, evening and night the west slope is 2–6° warmer than the east slope. The maximum temperature of the day occurs at about 4 p. m. This rather odd distribution of temperature is caused by the attitude of the western slope to the rays of the sun. Exposed as it is, it is shaded in the morning and it is not until late afternoon that the rays of the sun strike it at a high angle and raise the temperature to the maximum point. At night this slope is somewhat warmer than the east-facing slope. This is because the sparse vegetation, the relatively large amount of exposed rock, and thin covering of mold and forest debris on the west-facing slope permit a great degree of heat radiation at night.

During late spring and summer the west-facing slope is consistently warmer than the east-facing one (fig. 9B and C). In general, the difference is small, only 1–4°, this being due to the relatively greater amount of heat-consuming moisture transpired by the more dense vegetation on the east-facing slope. As in winter, spring, and autumn the maximum day temperatures occur at about 11 a. m. on the east slope and at about 4 p. m. on the west slope.

Comparison of Temperatures on Open Glade (Sta. C-1) and Closed Glade (Sta. C-2).—In winter, early spring, and autumn the open glade is usually 3–8° warmer during the day than the closed glade (fig. 10A, B, D), an obvious condition when one remembers the barren nature of the open glade. At night during these seasons it is from 1 to 4° cooler than the closed glade where the considerable abundance of junipers tends to make the air more quiet. A denser covering of mold and litter on the forest floor prevents rapid heat radiation which takes place on the barren open glade.

In summer, however, the open glade is constantly warmer than the closed glade (fig. 10C), being from 3 to 8° warmer between 9 a. m. and 7 p. m. and usually 1–4° warmer during the night and early morning. Normally it would be expected that the barren nature of the open glade would favor rapid heat radiation and that it would be cooler than the closed glade at night. However, a canopy of broad-leaved trees cover the closed glade during the growing season, which, together with numerous herbaceous plants on the forest floor, create a more equable climate.

History of the Land Use of the Area

In order to interpret the relatively complex flora inhabiting the area at present it was found necessary to learn the use of the land from facts revealed by the area itself. The history was begun as near as possible from the time when the land was first occupied by the white settlers emigrating from the East up to its present use as a wildflower reservation.

Use was made of data obtained from field notes taken on the area, and of documentary evidence offered by an abstract to the title of the land. Old trees were important sources of information concerning the aspects of the original flora. The younger trees served as indicators of changes in environment during the time that the area has been occupied by white man. A survey and map of tree stumps revealed the age of living trees of like diameter and also provided a definite record of the former use of the land. The abstract to the land title proved valuable by supplying the dates on which the parcels were granted to the first settlers. It also indicated the dates on which the land fell into the hands of the various families and finally the present institution, the Missouri Botanical Garden. The uses to which the various portions of the area were put, together with the time and intensity of use, were compiled in fig. 3.

The area is composed of two parcels of land which have had separate title histories up to the time that the Missouri Botanical Garden acquired them (fig. 3). A small portion of the area, on Cliff Ridge, represents part of an eighth section granted by the United

States to Edward J. Roberts on July 13, 1853. In 1881 it became the property of James B. Miles. The larger portion of the area is a part of the quarter section granted by the United States to William M. McPherson on June 19, 1851. Later the property was transferred to Powell; from Powell to Knapp in 1854; from Knapp to Crews in 1858; and from Crews to North in 1880. On March 12, 1925, both parcels of land were included in the area bought by the Missouri Botanical Garden.

An inspection of the area shows that it has been used in the following four ways, arranged progressively according to the degree to which the practice has altered the vegetation: (1) grazing, (2) light cutting over and grazing, (3) deforestation and grazing, (4) deforestation, cultivation, and grazing.

Grazing.—A survey of the area as a whole revealed it to have been generally and quite intensely grazed over. Though certain of the more ancient typical forest trees, oaks, hickories and maples, show decided preferences in their distribution, many younger specimens have a general distribution suggesting uniform conditions throughout the area. Such trees as red cedar *(Juniperus virginiana),* slippery elm *(Ulmus fulva)* and redbud *(Cercis canadensis)* are generally distributed and have been noted to invade local forested areas upon the advent of grazing.

Although it is evident that grazing is only one of the factors which have altered the vegetation of the area as a whole, there is a portion, representing slightly less than half the total expanse, on which grazing has been the only altering factor (fig. 3a). This fact is expressed by the total absence of stumps in a tract which contains an appreciable number of very old trees, obviously members of the virgin flora for their trunk diameters are comparable to stumps of trees calculated to be 175 to 260 years of age. These old trees have tall straight trunks and form a high canopy which, however, is broken in many places where individuals have died. Numerous dead specimens and standing ''snags'' are to be found, and many decaying trunks lie on the forest floor. Judging from the habit of the old trees, the aspect of the virgin forest was, for the most part, more closed and densely shaded. The present light open aspect of the forest suggests that a change of environment has taken place in a relatively short time. Throughout this plot there is a marked predominance of the group of trees referred to earlier in this account as indicative of intensive grazing. Counts of the annual growth rings of red cedars are perhaps alone the best indicator of conditions accompanying grazing of local forest areas. Several counts were made on trees from different points of the plot, and 30–40 years was found to be the average age. Allowing 10–20 years for grazing to alter the habitat sufficiently to encourage invasion by the red cedar and other heliophilous trees, it becomes evident that grazing was begun here shortly after the land was acquired by Joseph North in 1880. Grazing was practiced over the whole area up to the time that it was bought by the Missouri Botanical Garden.

Light Cutting-over and Grazing.—A small portion of the area, that immediately bordering the old pasture on the east slope of Ledge Ridge and extending a short distance down the slope toward the ravine, was lightly cut over during the period that the Arboretum was maintained by government-supervised transient labor. These recently cut stumps have supplied data concerning the ages of the forest patriarchs, and have offered some idea as to the approximate ages of stumps and trees found elsewhere on the area. The removal of many old trees has produced a poor canopy of foliage and has made the forest here very open, almost park-like. The rich mold on the forest floor has proved to be an excellent seed bed, and a dense thicket-like growth of shrubs and saplings forms a lower stratum of vegetation. In addition to the older trees of the group which have invaded under grazing conditions, many seedlings of these species originated during the period following cutting-over and the resultant increased light on the forest floor (see fig. 3b).

Deforestation and Grazing.—Two portions of the area, which when combined represent approximately half of the whole, have obviously been deforested (fig. 3, c, d). Many stumps are to be found here, all of a uniform age and none from old trees. The cut-over portion represented on Cliff Ridge (fig. 3d) is divisible into two parts, each having been deforested at a different date. The portion representing the land formerly belonging to James Miles was apparently deforested about 60 years ago. Though no trees were cut to obtain counts of annual growth rings, comparison of the trunk diameters with those of other young trees of known age warrants this statement. The stump remains found here are in poorer state of preservation than those of more recently deforested portions, but the diameters of the stumps place the entire former vegetation in the class of virgin flora. When the approximate age of the trees was compared with the title to the land it was found that this portion had been cut over about the time that the land was bought by James Miles.

The second, smaller portion of the deforested area on Cliff Ridge formerly belonged to Joseph North. The annual rings of several of the young trees now growing there were counted and showed the trees to be approximately 40 years old. The stumps, an undeterminable species of oak, found in this portion are in a better state of preservation than those of the trees cut from the Miles property. The age of the trees, together with the better state of preservation of the stumps, indicates this portion to have been more recently cut over than that on the Miles property, some 10–20 years after it was acquired by Joseph North.

It is evident that both portions have been grazed over quite intensely, for numerous islands of red cedar, slippery elm and redbud occur where the live stock succeeded in checking the rapid growth of the encroaching second growth of the forest.

Deforestation, Cultivation and Grazing.—A study of the plot on the east slope of Ledge Ridge (fig. 3c) has shown it to have been deforested and afterwards probably cultivated, for no stumps have been found there. Later on, and evidently for quite a period of time, it was apparently grazed and burned at intervals. A great number of the oaks and hickories now growing on the site exist as clumps composed of two to six trunks. This feature suggests that an old pasture already having a fair growth of seedling trees had been trampled by the hoof of livestock, or burned off, causing the original stem to die and numerous basal sprouts to spring up. The annual growth rings of several of these trees were counted and showed an average of 21. It is known that the site was still maintained as a pasture at the time of its purchase by the Missouri Botanical Garden in 1925. Relatively older trees, 40–60 years old, which border the plot on either side, have low limbs spreading into the clearing, indicating development as marginal trees. This fact places the clearing of this plot shortly after its purchase by Joseph North in 1880.

Vegetation

The arborescent flora is a complex one composed of 28 genera and a total of 40 species. As noted previously, the large number of species and the relatively wide distribution of many of them over the area may, perhaps, be best attributed to human occupation rather than to natural causes.

METHOD OF STUDY

The complexity of the vegetation suggested that rather intensive methods should be applied to its study in order to secure a complete picture of the distribution of all the component genera and their species. A series of five 150-foot belt transects was run across the area at 150-foot intervals in order to obtain a complete and detailed map of the trees and shrubs. Because of the wide range of genera and species represented in the flora, and because of the presence among them of many small trees and shrubs considered as being valuable indicators of various abnormal conditions, practically no attempt was made to divide the flora into size classes on the basis of actual field measurements. However, record of the relative sizes of the various consistently large specimens was kept and is discussed below. Data obtained from these individual maps were arranged in graphical form. The survey of stumps used in the study of the land use of the area has also served in interpreting the relics of the virgin forest flora.

Belt Transects.—The transects were mapped by plotting, in linear fashion, a series of 50-foot quadrats across the area. Three such lines of quadrats were plotted adjacent to one another, thus forming a belt transect 150 feet in width across the area (fig. 11). Individual quadrats were marked with flagged staffs, oriented transverse to the area with a compass. Distances were paced off. The number of each species represented in the quadrat was counted in turn and noted in corresponding quadrats on individual maps. Figures 13–17 show species in each belt transect, together with their respective distributions across the area. Species having a similar distribution have been grouped together.

On the basis of the belt-transect maps and graphs showing the density of each species in the different belt transects, a composite map has been prepared showing the grouping of the species into associations and associes and their areal extent (fig. 12).

The terms, association, associes, and dominant, used in discussion of the vegetation in this study, have been used in the sense originally applied by Weaver and Clements.[12]

DISCUSSION

As stated above, the complex nature of the vegetation of the area is essentially a condition resultant of intensive grazing. Likewise,

[12] Weaver, J. E., and F. E. Clements. Plant ecology, pp. 43–54. New York. 1939.

mention was made of a class of trees locally indicative of pastured forest land. It seems essential at this point to review the succession of conditions leading to the present state of the vegetation of the area.

Judging from the habit of the various scattered ancient forest trees, it is apparent that the aspect of the local forests before the advent of man was, for the most part, open. The trees were widely spaced. The canopy of foliage was quite well developed and gen-

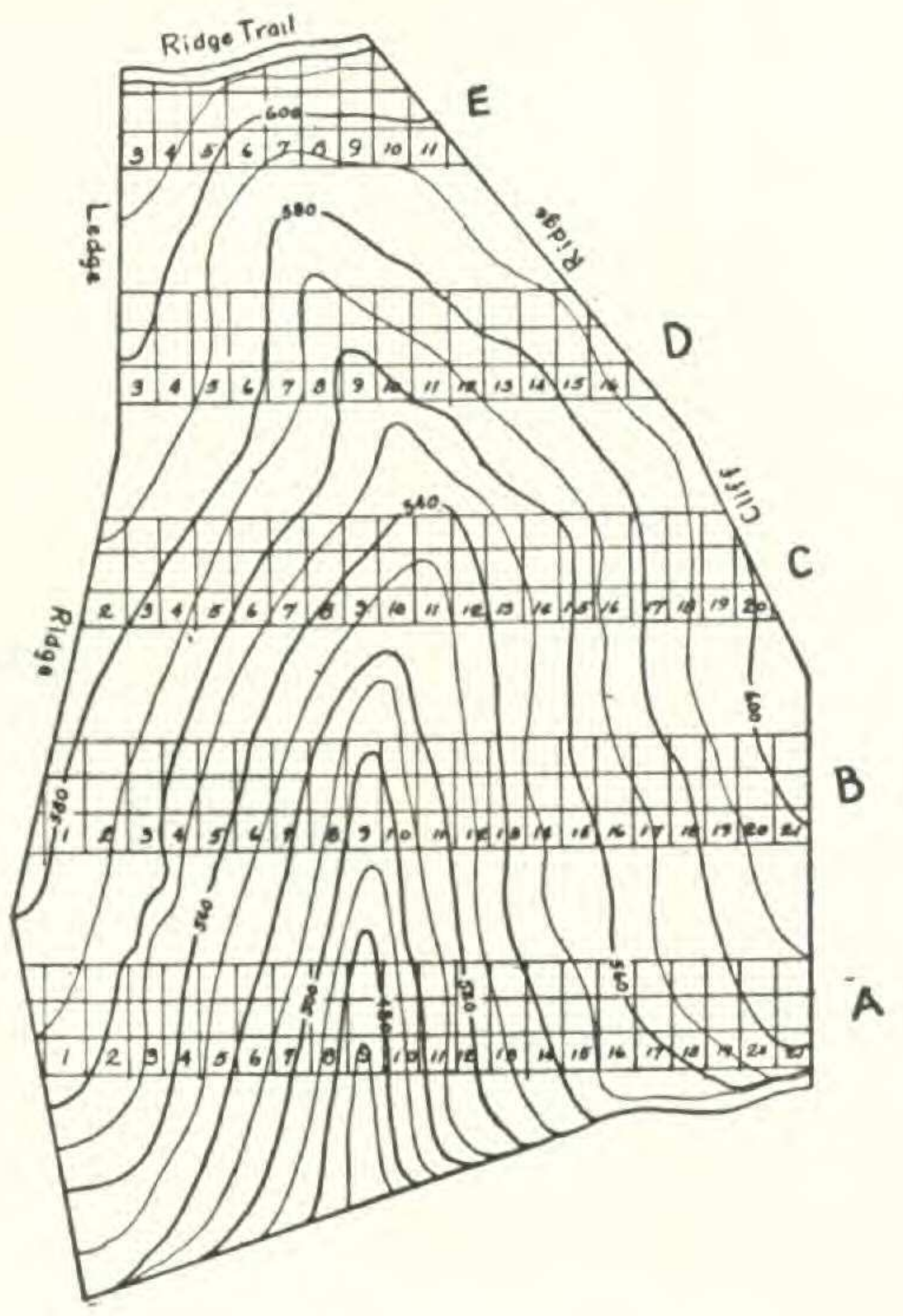

Fig. 11. Showing location of belt transects.

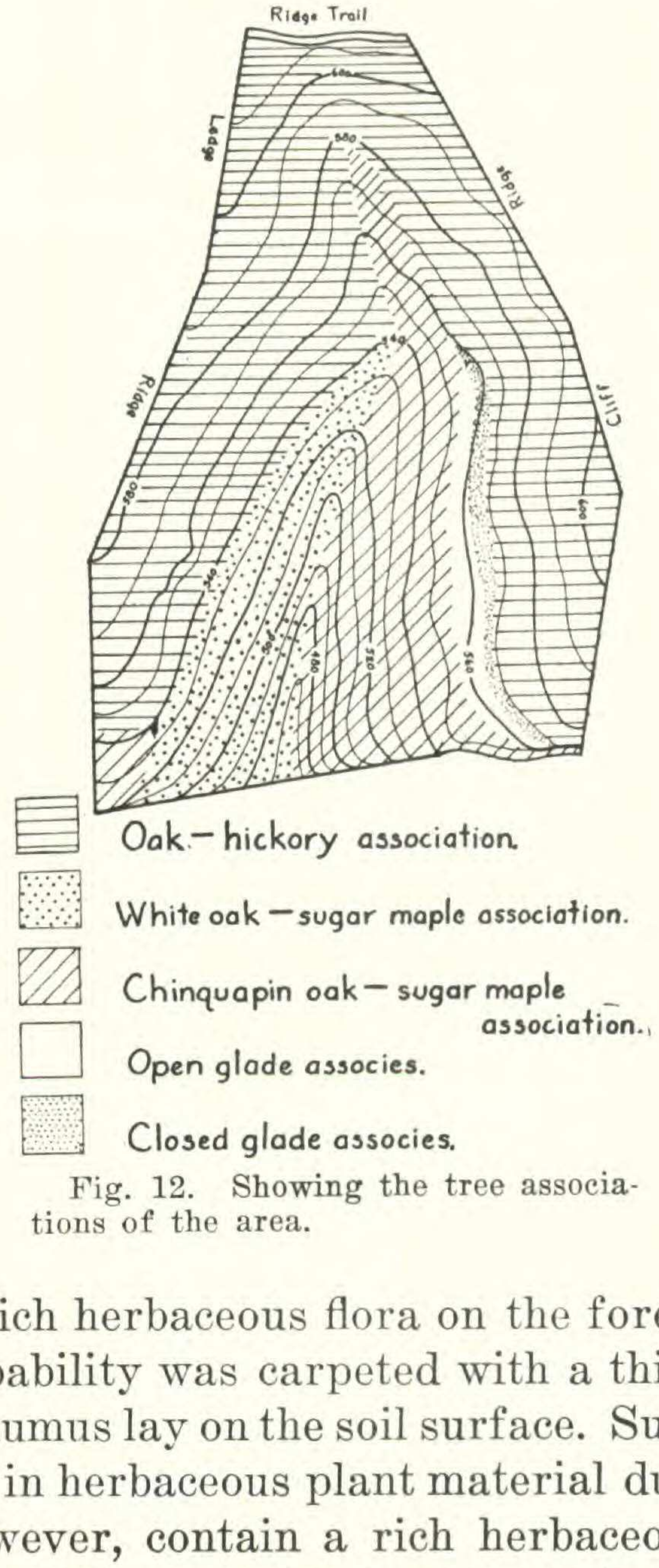

Fig. 12. Showing the tree associations of the area.

erally excluded the growth of a rich herbaceous flora on the forest floor. The forest floor in all probability was carpeted with a thick mat of litter, and a thick layer of humus lay on the soil surface. Such forests, though they may be poor in herbaceous plant material during the summer months, do, however, contain a rich herbaceous spring flora. It is not unlikely that the early landowners took advantage of this fact and turned their stock into the forests in the spring to forage on the fresh, succulent herbs. They were probably also quick to learn that by burning away the thick mat of litter on the forest floor, greater numbers of herbs could be induced to grow and that even certain grasses entered burned-off areas. Fire as an agent soon destroyed the layer of humus protecting the forest floor.

What little remained after the ravages of fire was stirred up by the cloven hoofs of the cattle, and, becoming an easy prey to the erosive power of heavy spring and summer showers, it was washed from the ridges and the slopes into the ravines and thence down to the river. Lacking the blanket of humus and litter the forest soils rapidly lost their moisture during the common late summer droughts. Competition for moisture among the trees became keen, many less sturdy individuals succumbing in order to balance this new deficit in water supply. The death of individuals left relatively large open "islands" in the forest canopy through which the rays of the sun could readily penetrate and thus intensify the xeric conditions already initiated. Continued grazing in the forest brought about even more erosion. More trees died, being unable to compete with their more sturdy kin for the necessary water with their roots bare.

A vegetational adjustment became imminent to prevent the complete denudation of the land. At this stage there was a marked influx of heliophilous plants formerly excluded from the forest. These plants, predominately red cedar *(Juniperus virginiana)*, slippery elm *(Ulmus fulva)*, and redbud *(Cercis canadensis)*, persisted. They were able to endure the late summer droughts and rigorous winters when the soil cover was scant. When the area became the property of the Missouri Botanical Garden grazing of forested areas was discontinued. The soil cover was no longer disturbed, and forest fires no longer reduced the protective layer of leaves and litter deposited by the trees each autumn. In a short time the heliophilous population matured, forming a lesser canopy of its own. Since the forest floor was shaded, a new carpet of humus and litter developed. The soil was once more cool and moist, permitting the origin and establishment of a new generation of the virgin flora. With this condition well in mind the complexity of the vegetation, previously referred to, becomes obvious when coupled with the wide range of habitats created by the geology, physiography and soils of the area.

An attempt was made to sort the various species into associations and associes on the basis of data secured from the graphs of the belt transects. However, the group of three heliophilous plants, previously referred to, appeared again as one to be dealt with before the true picture of the vegetational distribution could be composed. The density of the individuals comprising this group tends to mask any suggestions of association between the remaining species. The grazing conditions under which they have invaded the area and have become established have been discussed in considerable detail in a previous paragraph. In addition to these three species there may also be added: honey locust *(Gleditsia triacanthus)*, wild plum *(Prunus americana)*, black haw *(Viburnum rufidulum)*, and prickly ash *(Zanthoxylum americanum)*.

Three members of the heliophilous group tend to confine themselves to characteristic habitats, though, for the most part, they have a general distribution. Red cedar exhibits a decided preference for alkaline soils, and the oldest and healthiest specimens are to be found on the west slope of Cliff Ridge where the thin soil cover causes it to be influenced by the underlying dolomitic limestone rock strata. The black haw is essentially a small tree, loving open, rocky situations. The belt-transect graphs indicate it as being particularly distributed on the west slope of Cliff Ridge, where it has been shaded out by the more rapid growth of such large heliophilous trees as red cedar and slippery elm. Its present distribution is due to the open, xeric nature of the west slope of Cliff Ridge, maintained naturally by the southwestern exposure to the more or less drying, prevailing winds. It is probable that this area served as a center of distribution of the black haw to the east slope of Ledge Ridge and likewise to the pasture areas on either ridge. Prickly ash tends to prefer the more equable climate offered by habitats on the east slope of Ledge Ridge for it is here that fine mature specimens have developed. Like other members of this group, however, it will endure a wide variation in habitat and is rather generally distributed over the area.

With the above group of heliophilous plants withdrawn from consideration, the task of grouping the species into associations becomes comparatively easy. Inspection of the belt-transect graphs shows that it is possible to arrange the various genera and species of trees into three principal groups, two of which contain subordinate phases. A group, predominately oaks and hickories, shows decided preference for the ridges where it forms an oak-hickory *(Quercus-Carya)* association. Two developmentary phases are represented within this group. A second group dominated by white oaks and sugar maples, forming a white oak-sugar maple *(Quercus alba-Acer saccharum)* association, shows preference for the lower

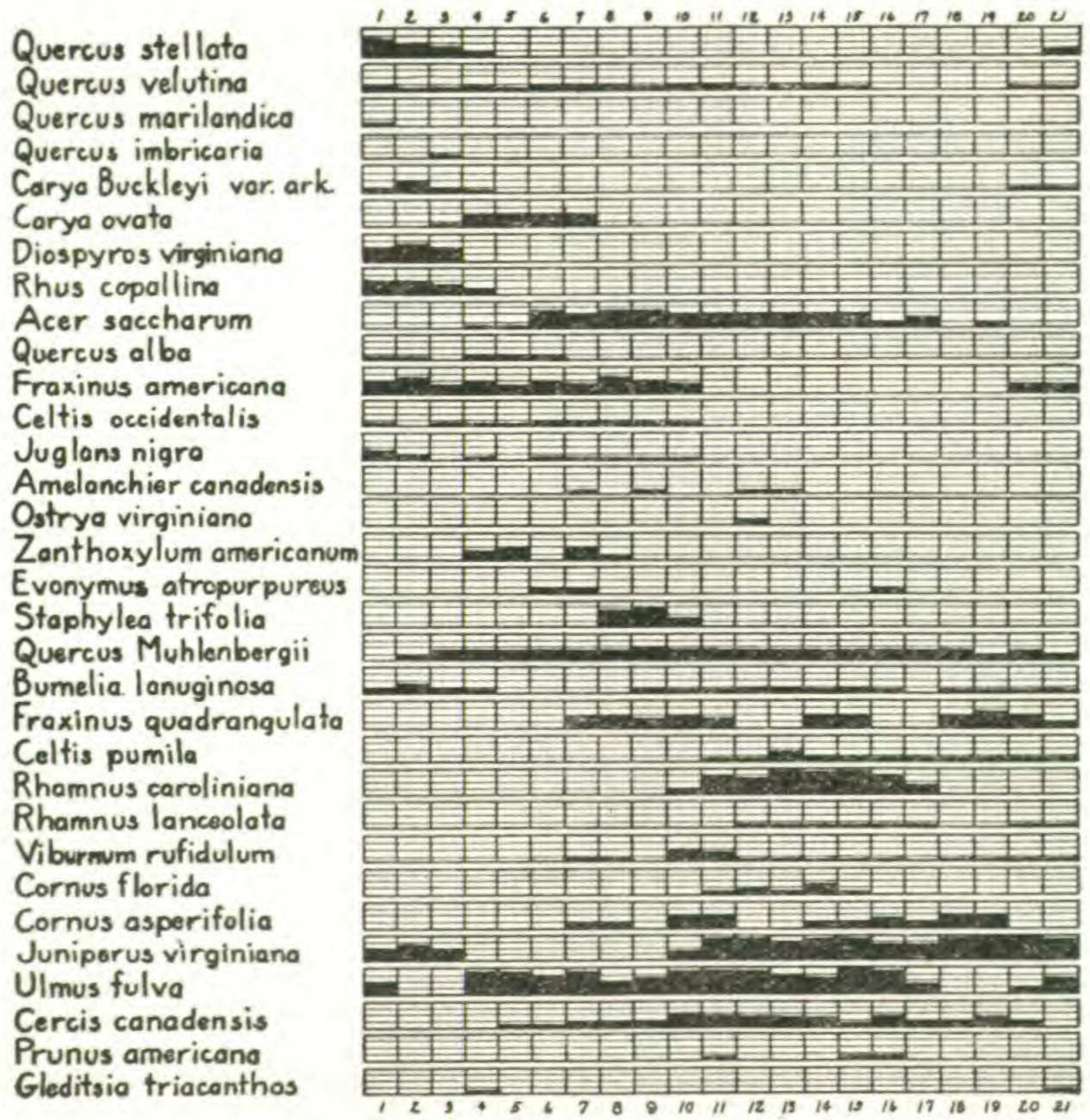

Fig. 13. Showing distribution and density of species in belt transect A (see fig. 11).

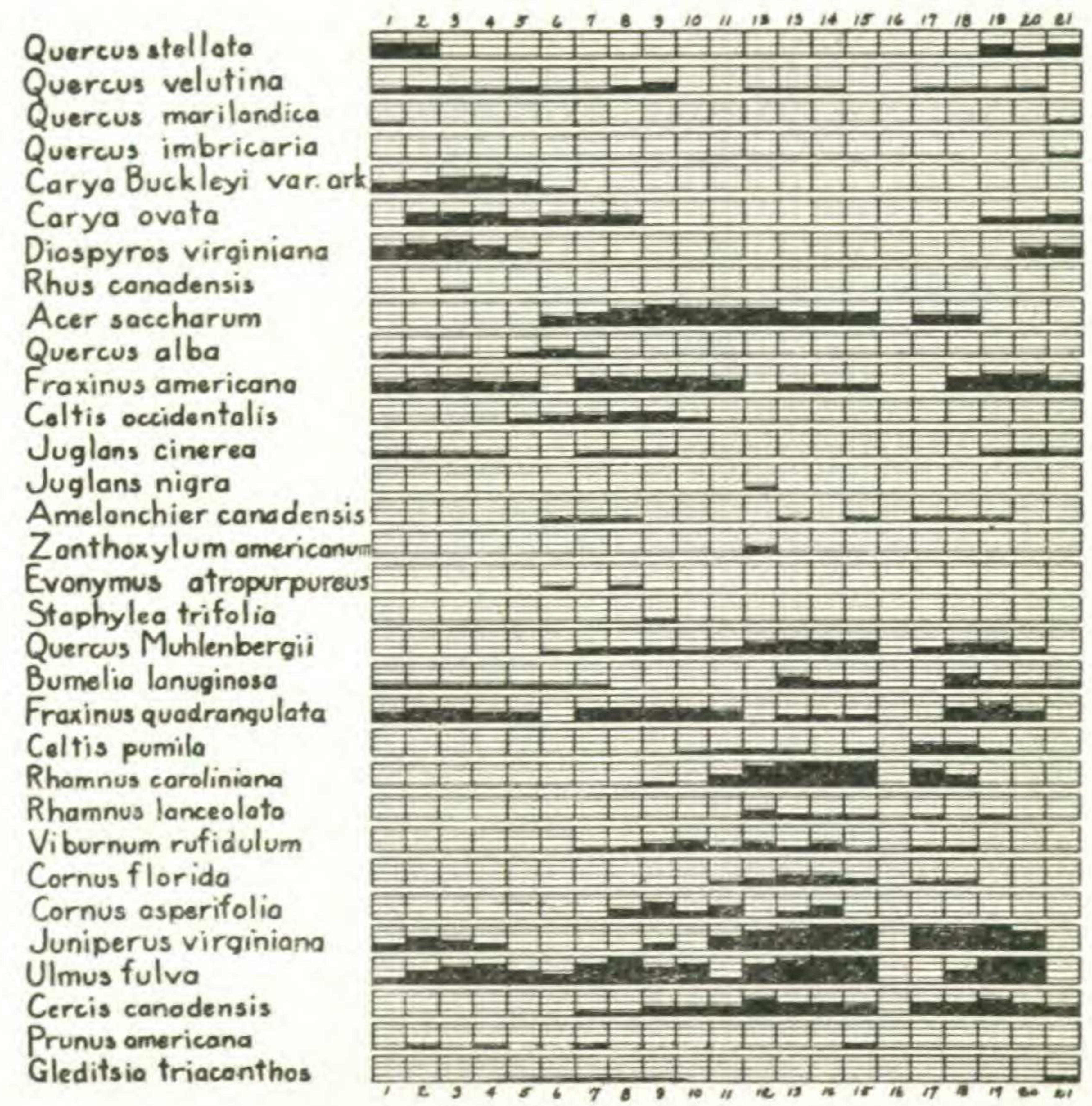

Fig. 14. Showing distribution and density of species in belt transect B.

Unit 1 = 0–1.4 plants; 2 = 1.5–2.4 plants; 3 = 2.5–4.4 plants; 4 = 4.5–7.4 plants; 5 = 7.5–11.4 plants; 6 = 11.5–16.4 plants; 7 = 16.5–22.4 plants; 8 = 22.5–29.4 plants.

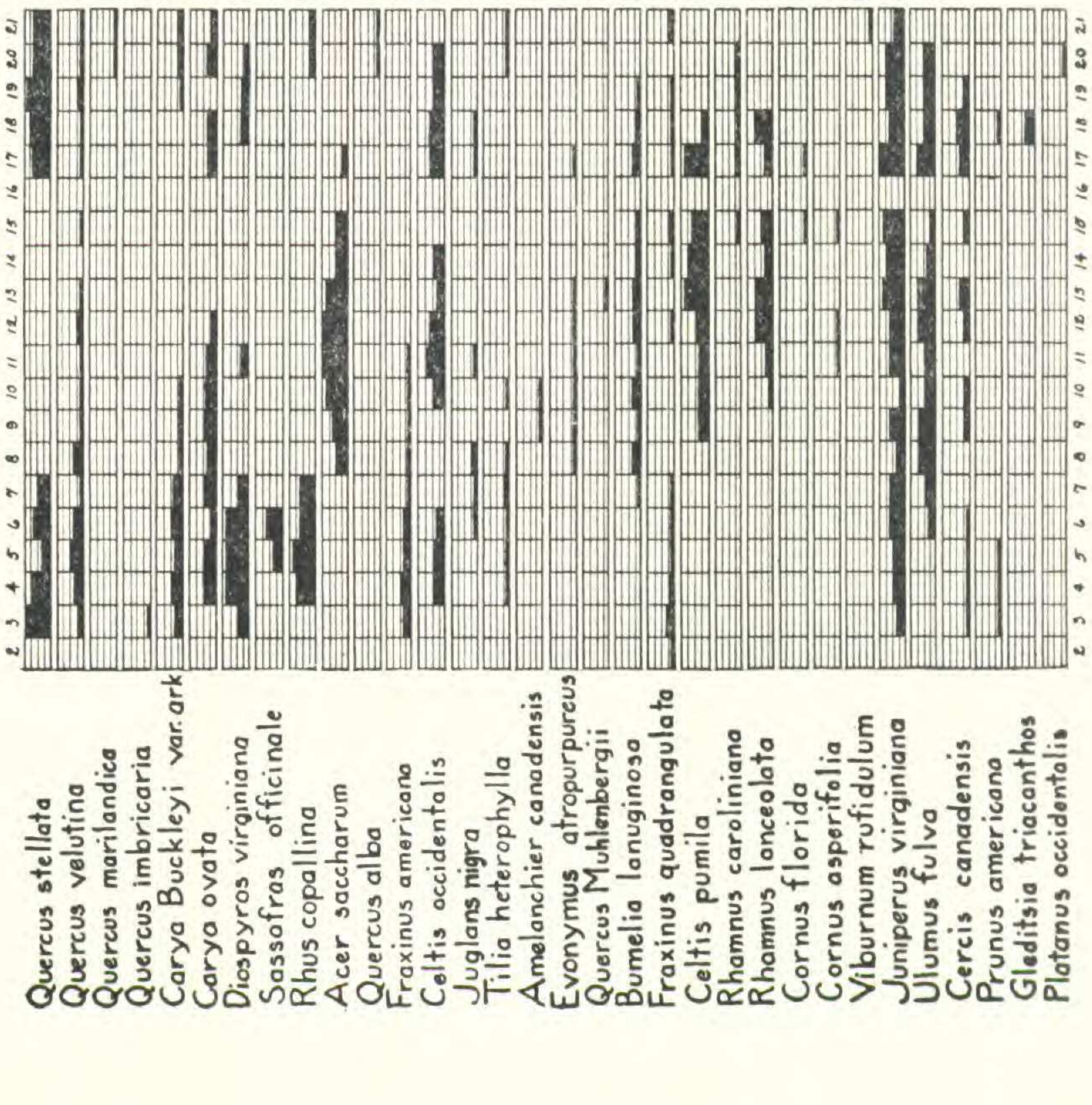

Fig. 15. Showing distribution and density of species in belt transect C.

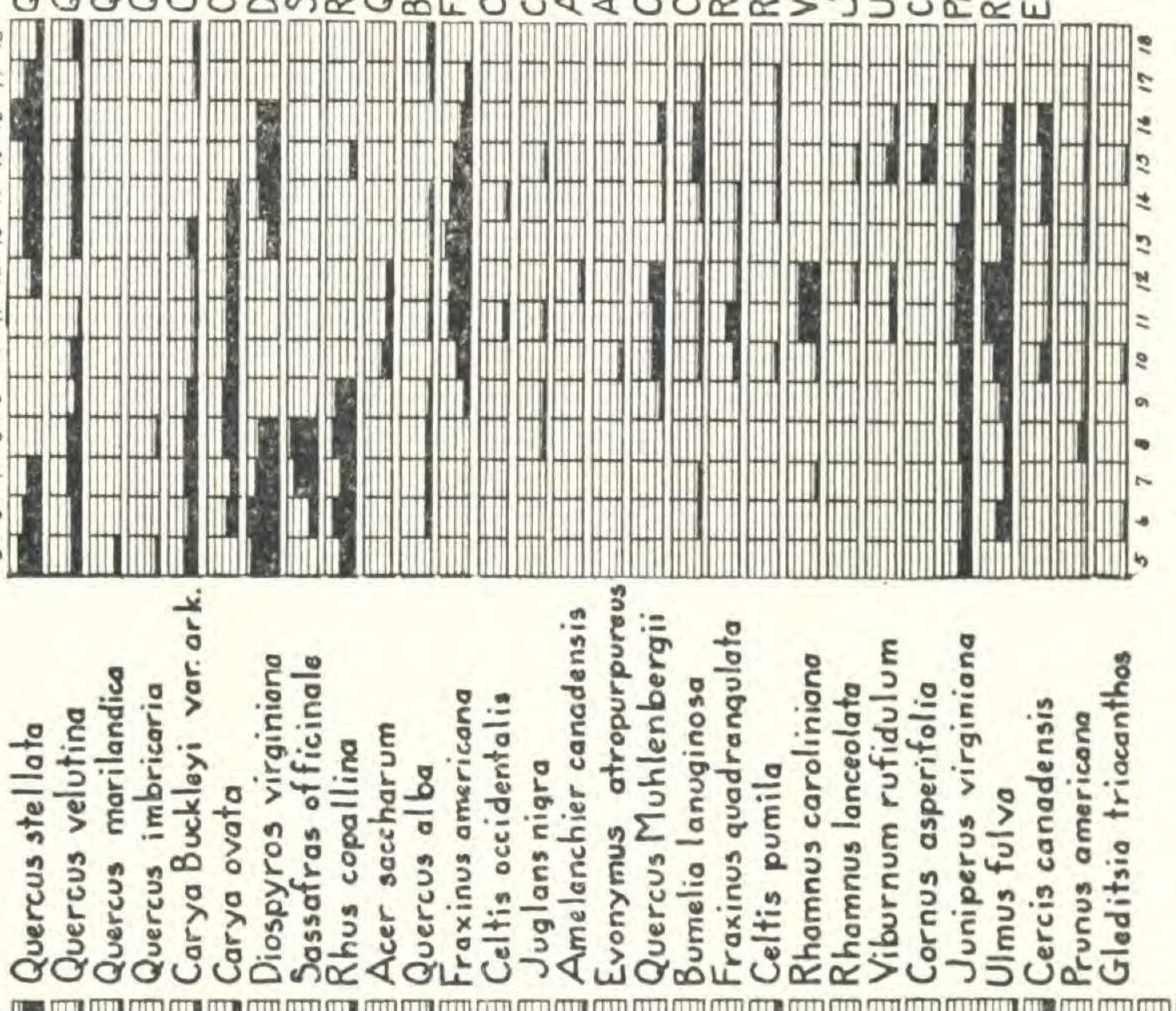

Fig. 16. Showing distribution and density of species in belt transect D.

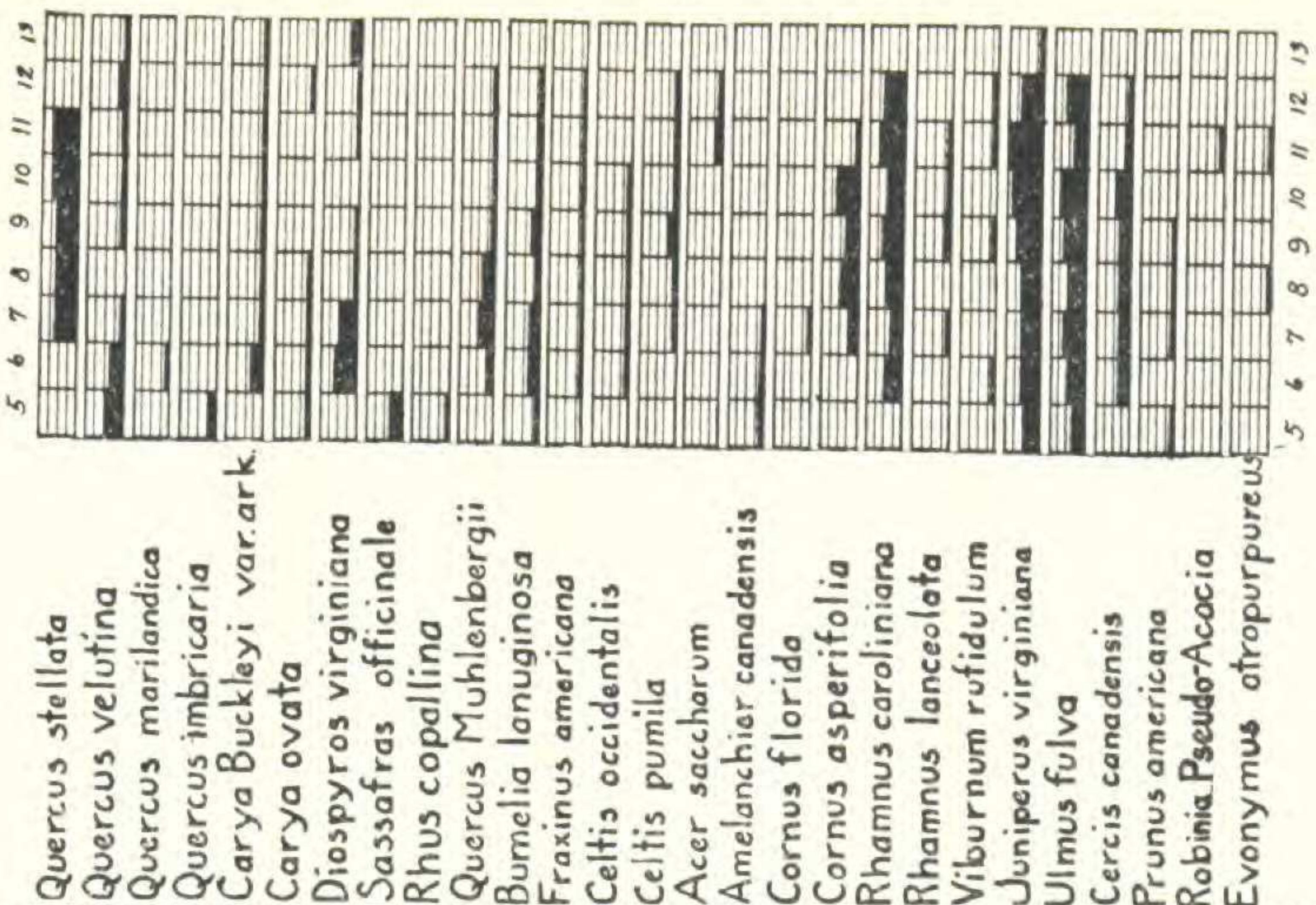

Fig. 17. Showing distribution and density of species in belt transect E.

slopes of Ledge Ridge. A third association is distinct in preferring the barren, rocky exposure of the west slope of Cliff Ridge. It is dominated by a growth of chinquapin oak and sugar maple. This association has a subordinate phase, a group of trees dominated by red cedar which prefers the more xerophytic environment of the glade.

The Oak-Hickory *(Quercus-Carya)* Association.—Grouped into this association are: post oak *(Quercus stellata),* Ozark hickory *(Carya Buckleyi* var. *arkansana),* black oak *(Quercus velutina),* black jack oak *(Quercus marilandica),* and the shingle oak *(Quercus imbricaria)* (figs. 13–17). The status of these trees within the association is not one of equal importance. A study of the belt-transect graphs indicates that the post oak and Ozark hickory are dominant. As stated above, these graphs are purely a study of density and distribution, and give no indications of size and age.

On Ledge Ridge and that portion of the ridge at the head of the valley, large trees are consistently white oak, black oak, and Ozark hickory. Judging from the ages of stumps of similar diameter elsewhere in the area their age varies between 150 and 200 years. This places them in that group comprising the relics of the virgin flora in which they may serve as indicators of the former climax.

On Cliff Ridge the conditions are not so easily read. The total deforestation of this portion (fig. 3c) has left no relic trees of the virgin forest. Although numerous stumps of trees, approximately 150–200 years old, are to be found, they were in a rather poor state of preservation and all that could be identified were oaks. The relatively great intervals at which the stumps occur seem to suggest that the trees were of stout, spreading habit such as that commonly developed by ridge-top post oaks. The probability of the former climax being composed essentially of post oak is supported by the fact that this ridge is for the most part very narrow. It receives little protection from hot dry winds by the surrounding ridges, and its high isolated position does not permit water to linger long either on or in the soil. Temperature recordings show that in summer this ridge is consistently warmer than the valley or lower habitats, and that during midday and early afternoon it is usually 5–8° warmer than a comparable station in the valley (fig. 8C). The present vegetation is predominantly of post oaks approximately 30 years old. Black oaks, white oaks, and Ozark hickories occur in minor numbers (figs. 13–17). Seedling trees are absent for the most part.

These facts seem to indicate the revival of a former post oak climax on this ridge. Although post oaks also occur in great numbers on Ledge Ridge (figs. 13–17), their distribution is different from that observed on Cliff Ridge. On Ledge Creek it is almost totally limited to the boundaries of the old deforested and pastured plot (figs. 3, 12), and exists as an associes, a stage leading to the development of the oak-hickory climax association.[13] The belt-transect graphs show a relatively high per cent of black oak, white oak, and Ozark hickory also composing this old pasture flora (figs. 13–16). These are, for the most part, young trees 5–10 years old, while the older post oaks are 21 years old, a fact which indicates that the oak-hickory climax common to Ozark ridges is rapidly becoming dominant.

An even earlier stage of the development in the succession from cleared ridge lands to an oak-hickory climax association is represented by the pioneer plants, now almost completely dominated by the post oak associes (fig. 12). Included in this ''old field'' associes are persimmon *(Diospyros virginiana)*, sassafras *(Sassafras officinale)*, and shinning sumac *(Rhus copallina)*. With the exception of the persimmon, which has a more general distribution, these occur as small ''islands'' only partially invaded by the more advanced stage of the post oak associes. A comparison of the composite map of the vegetation (fig. 12) with the map of the areal distribution of the various degrees of soil acidity (fig. 6) shows a very close correlation between the environment of these ridge-top trees and areas of high degree of soil acidity. The white and black oaks of this association have an indifferent attitude toward degree of soil acidity and appear quite generally over the entire area. The remaining members have distributional boundaries almost identical with the areas of acid soils. These correlations support Steyermark's conclusions concerning the vegetation of the Ozarks in Missouri.[14] No correlation could be found between this association and the soil types (fig. 5), nor could it be identified with any particular outcropping of the various rock strata (fig. 2) which at this point are deeply overlain with soil (fig. 4, a, b).

The White Oak–Sugar Maple *(Quercus alba–Acer saccharum)* Association.—The belt-transect graphs reveal a second prominent group of trees which conspicuously prefer the exposure of the east

[13] Steyermark, J. A. Studies of the vegetation of Missouri—I. Bot. Series, Field Mus. Nat. Hist. 9: 351–475. 1940.

[14] Ibid., p. 405.

slope of Ledge Ridge (fig. 12). Unlike the neighboring ridge, this association is represented by a large group of species: white oak *(Quercus alba)*, sugar maple *(Acer saccharum)*, white ash *(Fraxinus americana)*, black oak *(Quercus velutina)*, shagbark hickory *(Carya ovata)*, hackberry *(Celtis occidentalis)*, burning bush *(Evonymus atropurpurous)*, black walnut *(Juglans nigra)*, shadbush *(Amelanchier canadensis)*, and bladder-nut *(Staphylea trifolia)* (figs. 13–16). As indicated in the discussion of the preceding association, it is not possible to assign dominance to any several species solely on the basis of facts represented in the belt-transect graphs. This association is fortunate in having a considerable number of virgin trees. A comparison of their trunk diameters with those of stumps of readable age elsewhere in the area places all of these trees between 160 and 200 years old, in that age class which is conspicuously composed of virgin trees. They are all straight-boled and form a relatively high canopy broken where many of them died out when the environment was altered by grazing. Of the large and older trees, white oaks and sugar maples are dominant. Aged, living sugar maples are not common in the area, probably because they were unable to endure the conditions brought about by grazing, namely, the depletion of the thick layer of litter and humus on the forest floor. The association has a well-developed understory of bladder-nut *(Staphylea trifolia)*, spice bush *(Benzoin aestivale)*, prickly ash *(Zanthoxylum americanum)* and burning bush *(Evonymus atropurpureus)*. Seedlings and saplings of white oaks and sugar maples abound.

An attempt to correlate this association with the various environmental factors reveals that it corresponds most closely with the limits of alkaline soils of the lower portion of the east slope of Cliff Ridge (fig. 6). This association prefers a pH range from 6.8 to 8.5. Here the degree of acidity of the soil is affected to a greater extent by the underlying dolomitic limestone because the soil layer is considerably thinner, varying from 8 to 14 inches in depth. The association may be further correlated with the limits of the "rough stony land" on this slope (fig. 5). The eastern exposure of the slope on which this association has developed has caused it to assume a mesophytic aspect. Being exposed to the east as it is, the slope receives the direct rays of the sun only in the morning before the air has been heated up. Thus the sun has a less burning effect upon the foliage of the trees during the summer drought periods. The slope is shaded from the rays of the sun during the heat of the day, from

2 to 4 p. m. The temperatures recorded on the slope are consistently from 1 to 4° cooler than those of a comparable position on the western slope (fig. 9C). The greater equability of this environment as compared with the distinctly xeric habitat on the west slope is manifest in a more succulent herbaceous flora. Humus and litter have collected in a thicker carpet on the forest floor, thus protecting it from excessive erosion and likewise serving as a moisture-conserving mulch.

The Chinquapin Oak–Sugar Maple *(Quercus Muhlenbergii–Acer saccharum)* Association.—As previously stated, this association inhabits the western slope of Cliff Ridge (fig. 12). The dominant trees are chinquapin oak (*Quercus Muhlenbergii)* and sugar maple *(Acer saccharum).* Other important members of the association are: red cedar *(Juniperus virginiana),* chittim-wood *(Bumelia lanuginosa),* black oak *(Quercus velutina),* and blue ash *(Fraxinus quadrangulata).* Trees playing a minor part in the association are white ash *(Fraxinus americana)* and black walnut *(Juglans nigra).* Trees and shrubs forming the rich understory are: dwarf hackberry *(Celtis pumila),* redbud *(Cercis canadensis),* Indian cherry *(Rhamnus caroliniana),* black haw *(Viburnum rufidulum),* buckthorn *(Rhamnus lanceolata),* flowering dogwood *(Cornus florida)* (figs. 13–16).

The association has a light, open aspect, no canopy in a true sense having been developed. Relatively few of the dominant trees are actually dead though many exist in a poor state of health. A comparison of the trunk diameters with stumps of known age places the majority of the older specimens in the group of virgin trees. The habit of these trees seems to suggest that the aspect of this association has not been appreciably altered by grazing conditions. The fact that these trees have a lower and more spreading branching habit than that of the typical forest specimens in the associations previously described indicates that they developed under conditions very similar to the semi-xerophytic ones existing today, and may perhaps account for the slight damage suffered from grazing.

It is probable that even prior to the advent of human activities in the area, the soil cover lay thin on the bed rock beneath, and that though a rather rich herbaceous flora had developed it was necessarily xerophytic in nature. These facts are in accord when one remembers that the western exposure of this habitat leaves it relatively unprotected from hot, dry south and southwestern summer winds, and likewise raw, cold winter winds. The attitude of the slope causes it to have a high angle of incidence to the rays of the sun during the heat of the day, that is, from 2 p. m. to 4 p. m. This results in a temperature of 1–4° over that recorded at a comparable station on the east slope of Ledge Ridge (fig. 9). This xeric condition is intensified when the numerous thin-bedded phases and sand lenses incorporated in the rock strata are taken in consideration (fig. 1). These serve as drains through which percolating ground waters are rapidly conducted off, leaving little water in reserve for periods of drought despite the high organic content of the soil. As previously mentioned, the shallow depth of the soil has caused it to be exploited to a high degree by roots of trees and herbs, which necessarily means that it would be rapidly depleted of moisture regardless of the high content of organic matter. The relatively thin depth of the soil layer, together with its residual origin from the underlying dolomitic limestones, has favored the development of a typically alkaline soil (fig. 6) which is reflected markedly in the flora. Steyermark includes the dominant plants of this association in his list of plant indicators of alkaline soils.[15]

The Glade Associes.—The glade is a plant environment distinct from all other habitats presented by the area (fig. 1). The soil is very shallow, and numerous rock shelves are exposed, which, together with the conspicuous lack of trees over the greater part of its extent, give the glade a barren open aspect. Further inspection shows the position of the glade to be correlated with the extent of the outcropping of the upper, thin-bedded phase of the Cotter formation on this western slope. This suggests that the origin of the glade lies within the properties of this rock. In a previous paragraph this thin-bedded phase of the Cotter formation was characterized as being a highly porous and permeable rock. These features and the comparatively great depth, 7 feet, of this phase cause it to present a plant habitat with a wide range of seasonal conditions. The high porosity and permeability of the rock permit free movement of water. Early spring rains rapidly percolate through the rock or water may be drawn from it by rapid evaporation, having been brought to the surface by capillary action. This means that the rock creates an arid substratum during summer. In autumn and late winter another extreme is experienced. With the increase in precipitation and accompanying decrease in evaporative powers of

[15] *loc. cit.*, p. 407.

the atmosphere, the rock becomes literally saturated with percolating ground water. The sparse plant cover does not bind the soil in place against spring and later summer rains (fig. 7). The surplus of water in the bedrock beneath the soil in winter forces its way to the surface of the rock, where, acting as a lubricant and erosive agent, it also carries the soil away. The western exposure of this unique environment only tends to intensify the already extreme edaphic conditions. In summer the hot, dry, southern and southwestern winds, and the high angle of incidence of this slope to the rays of the sun during the heat of the day, create intensely desiccating conditions.

The Open Glade Associes.—Almost the entire area of the glade is open (fig. 12), appearing like a barren, rocky, upland meadow. These conditions have resulted in almost total exclusion of an arborescent flora. Over the greater part of its extent an herbaceous associes prevails, Missouri black-eyed Susan–bluestem *(Rudbeckia missouriensis-Andropogon scoparius).* Trees are excluded from the open glade, the arid summer conditions preventing the establishment of seedlings. However, several small ''islands'' of red cedars are trying to exist here.

The Closed Glade Associes.—The small closed glade is founded on essentially the same environmental conditions as those controlling the open glade. However, it differs from the open glade in being forested with a red cedar *(Juniperus virginiana)* associes. Other important trees are: chinquapin oak *(Quercus Muhlenbergii)* and chittim-wood *(Bumelia lanuginosa).* A well-developed understory is composed of Indian cherry *(Rhamnus caroliniana),* buckthorn *(Rhamnus lanceolata),* dwarf hackberry *(Celtis pumila),* black haw *(Viburnum rufidulum),* redbud *(Cercis canadensis),* and flowering dogwood *(Cornus florida).* This associes is distributed as a narrow band bordering the upper edge of the open glade associes (figs. 1, 12), and may be correlated with the uppermost portion of the thin-bedded phase of the Cotter formation and the basal sandy phase of the Powell formation (figs. 2, 12). Here the substratum of rock remains more moist since it lies adjacent to the massive rocks of the Powell formation which retains percolating ground waters considerably longer than the thin-bedded cotton rock of the Cotter formation. Humus is washed down upon the glade from the oak woods above it and is an important factor in increasing the soil moisture since it serves as both a reservoir of moisture and as a mulch. This increase in soil moisture has permitted the invasion of trees upon the glade edge. The extremely xeric conditions prevailing during the summer months, however, limits the habitat to occupation by drought-resistant species such as red cedar, chittim-wood, and chinquapin oak. Though a canopy of interlacing cedar boughs is well developed it is characteristically of a gauze-like texture, and permits abundant light to encourage the rich understory of small trees and shrubs.

These glade associes have, in all probability, been the least injured by grazing. The xerophytic nature of the open glade necessarily produces plants of a tough, leathery texture which offers little encouragement to cropping by animals. A thick mat of slowly decaying cedar needles prevents seeds of herbs from reaching a suitable stratum for germination. Thus it is evident that this associes was undisturbed by livestock. A portion of the associes was deforested (fig. 3c), but this caused little alteration of the flora aside from the removal of the virgin trees. Steyermark has shown how similar glades and rocky barrens in the Ozarks are invaded and dominated in part by red cedar and chittim-wood among other trees.[16] Dead or dying specimens are almost totally absent. It is evident that this associes exists today much as it must have before settlement of the region by white man.

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